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Resource limitation in brown hare (Lepus europaeus) populations.

RESOURCE LIMITATION IN BROWN HARE (*LEPUS EUROPAEUS*) POPULATIONS

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'The balance of nature' does not exist, and perhaps never has existed. The numbers of wild animals are constantly varying to a greater or less extent, and the variations are usually irregular in period and always irregular in amplitude. Each variation in the numbers of one species causes direct and indirect repercussions on the numbers of the others, and since many of the latter are themselves independently varying in numbers the resultant confusion is very remarkable.

Charles Elton, 1930.

ABSTRACT

In this thesis, the population dynamics of brown hares (*Lepus europaeus*) were studied in relation to the pattern of available food resources, in areas of intensive arable agriculture. This aimed to test the hypothesis that food resources limited these populations.

The carcasses of nearly 600 hares were collected from culls held at six estates in the February of 1993. The density of animals culled on each site was positively related with the combined area of winter wheat, plough, set-aside and stubble. The dominant component of the diet was winter wheat, and at the high density sites, females were heavier, with greater numbers of foetuses, and males had larger testes. However, an analysis of the age structure of the hare populations showed that recruitment was 45% lower than expected as a result of poor breeding success in summer. Computer models showed that a drop in recruitment of 45% would not drive the population extinct, but would create declines similar to those observed from game bag data since 1961.

Patterns of habitat change were also examined, and the major changes identified as the loss of crop diversity to the expanding area of winter wheat. These changes were analysed in relation to the foraging behaviour of hares, and it was concluded that large amounts of forage which would have been utilised by hares in summer, has been lost.

Further carcasses were collected between April and July in 1993 and 1994 to examine the diet and breeding success of hares in summer. The number of females pregnant and lactating was low, and both males and females were lighter in summer, and in poorer condition. The energetic demands of maintenance, reproduction and growth were estimated for winter and summer, and the levels of digestible energy and digestible nitrogen in the winter and summer diets estimated. The summer diet was less digestible than the winter diet, and this meant that , to meet the cost of reproduction in summer, the intake had to be at levels which were near the maximum for hares. However, intake could not be measured from these samples. It was concluded that the digestible energy content of the summer diet was limiting hare populations.

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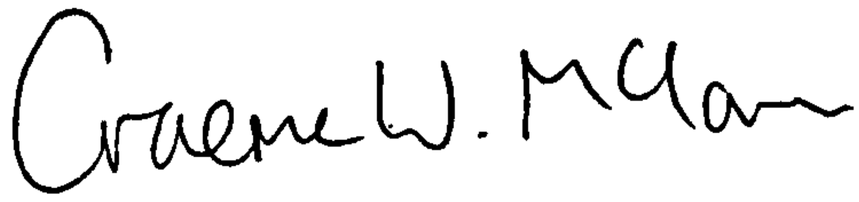
I would also like to thank the other members of the mammal research group, who number to many to mention, who have helped me, during the course of my PhD. I am also lucky to have a supportive and loving family, and I would especially like to thank my parents.

Finally, I would like to thank Kat, for her love and support.

DECLARATION

I declare that the work contained within this thesis is my own and has not been submitted in consideration for any other degree or award.



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INTRODUCTION

1.1 The study of animal abundance: a historical perspective

In 1906 there were an estimated 4,000 mule deer (*Odocoileus hemionus*) on the Kaibab plateau in North America, but by 1924 there were over 100,000; two years later the population had fallen by 60,000 animals (Lack 1954). This now classic example demonstrates the capacity for animal populations to change in response to changing conditions. In this case, increased numbers were brought about by the extermination of predators and the prohibition of hunting, and the decline by food shortage (Lack 1954). The potential that all animal populations have for increasing was first pointed out in an essay by the Rev. T.R. Malthus in 1798, in which he stated that animal populations can increase geometrically, and as a result, animal populations will increase up to the limit of food supplies if they are not limited by predation, disease or other factors (Elton 1930). The study of animal abundance is concerned with understanding the relationships between a population with an innate capacity for exponential increase, and the restraints imposed on it by the biological and physical environment. A considerable amount of research has attempted to address this problem. However, in order to review the important theories which have arisen from this work, it is first important to establish some definitions, as Sinclair (1989) points out, much of the debate surrounding the study of animal abundance is clouded by misunderstandings of the important concepts.

A ***population*** is normally defined as a group of coexisting individuals which interbreed if they are sexually mature (Sinclair 1989). The population size is determined by four parameters: births; deaths; immigration and emigration, which are normally expressed as rates (Begon, Harper & Townsend 1990; Sinclair 1989). The resulting balance between these rates sets the population size, and also determines if the population is at equilibrium (unchanging), rising or declining. As Malthus pointed out, a growing population will eventually reach a point where one or more particular factors start to limit the growth of the population, and the population size will then reach its ***equilibrium density***, when the rates of birth, death and immigration and emigration are balanced. A population which reaches an equilibrium density is said to be ***limited.*** The factors which determine when population growth stops are ***limiting factors***. The population may then be observed to fluctuate about the equilibrium density, as a result of perturbations or random variation in the four rates. The process by which a population returns to equilibrium density is ***regulation,*** and the factors which bring this about are ***regulating factors***. The crucial aspect of regulating factors is that they are ***density dependent,*** in that the strength of their action is related to the difference between the population size and the equilibrium density (Sinclair 1989). Begon, Harper & Townsend (1990) divide the factors which are responsible for limitation and regulation into ***resources*** - something an animal uses up (e.g. food) and ***conditions*** - something an animal needs but does not use up (e.g. the correct temperature). These are the definitions I will use in this thesis. The terms comprise the theory of density dependent population dynamics, which was first proposed by Nicholson in 1933, and neatly summarised by

Lack (1954), who stated 'Most wild animals fluctuate irregularly in numbers between limits that are extremely restricted compared with what their rates of increase would allow'.

Alternative to this view was that environmental factors controlled the number of animals in a density independent manner (Andrewartha & Birch 1954). In this model it is the shortage of time in which the population is increasing that limits the population, the population growth being cut back by environmental harshness, such as bad weather conditions (Andrewartha & Birch 1954). Andrewartha (1961), although not disputing the idea that, in certain circumstances, density dependent factors may operate, rejected the density dependent idea that populations fluctuate around an equilibrium density as untestable stating that 'It is clear that this conceptual model has little chance of helping the ecologist to explain the distribution and abundance of the species that he studies'. Thus arose the two contrasting schools of thought on population abundance.

The views of Andrewartha & Birch were supported by their own extensive field research, such as their study of *Thrips imaginis*, during which adult *T. imaginis* were counted every day for fourteen years in a large Australian garden (Andrewartha 1961). They found extensive seasonal variation in numbers, and related this to weather influences on food supply; they found no evidence of an equilibrium density. In the same year that Andrewartha & Birch set out their views in *'The Distribution and Abundance of Animals'* (Andrewartha & Birch 1954), a contrasting view was put forward by Lack in *'The Natural Regulation of Animal Numbers'*, where it was argued that 'the comparative stability of populations must be due to controlling

factors which are density dependent' (Lack 1954). Lack used evidence from studies which showed that population densities were constant from year to year, and also his observations of density dependent mortality in birds to back his arguments. It was also generally thought that a population which was not regulated would quickly go extinct. However, in 1954 there was little experimental evidence to show that populations displayed density dependence.

It is now clear that Andrewartha and his co-workers were determining population limitation, i.e. weather determined food abundance which determined population size, and the absence of an equilibrium was the result of the seasonal environment. In contrast Lack was concerned with regulation using evidence from relatively stable environments (Sinclair 1989). However, Andrewartha's ideas that populations could persist without density dependent regulation are now largely rejected (Sinclair 1989). Thus there is an important distinction between identifying the factors which limit a population, and determining if a population is regulated.

In terms of wildlife management, determining what limits the growth of a population is extremely important. However, as Sinclair (1989) points out, any factor that changes the number of additions or losses to the population will be a limiting factor, thus making it vital to determine the relative importance of each factor.

1.2 The relationship between herbivores and resources: are herbivores ever resource limited?

The most obvious factor which might limit a herbivore population is the availability of living plant material. Initial work in this area concentrated on determining the

amount of living plant material produced in an ecosystem (the primary production) and then measuring the amount consumed by herbivores: if herbivores are food limited, then consumption would be equal to primary production. In terrestrial ecosystems however, typically less than 10% of primary production is consumed by herbivores (see review in Sinclair 1975). This lead Hairston, Smith & Slobodkin (1960) to suggest that in general, herbivores are not food limited, but must be limited instead by predators, parasites or disease. However, as demonstrated by Sinclair (1975), plant species may not be equally abundant or nutritious throughout the year, and that this can have serious consequences for a herbivore population. Sinclair (1975) found that the primary productivity of the Serengeti grasslands of East Africa were related to rainfall, and that this resulted in large monthly variations in the quantity and quality of food available to the herbivore populations. By estimating the requirements of the herbivore populations, Sinclair found that during the dry season, food availability was lower than the requirements of the resident herbivores and concluded that 'this would be sufficient to limit herbivore populations' (Sinclair 1975). Therefore, although the total yearly productivity may be in excess of that consumed by herbivores, the pattern of productivity may result in periods of food shortage.

By making realistic assessments of food availability and requirements, periods of nutritional stress can be identified. However, in order to limit population growth, this stress must result in a declined productivity and/or an increased mortality of members in the population. Herbivores may have adaptations which overcome the seasonality of their environment. For example, greater kudu

(*Tragelaphus strepsiceros*) were found to exhibit a range of 'compensatory foraging responses' when food became scarce during the dry season in South Africa (Owen-Smith 1994). The responses included increasing the proportion of time spent foraging, increased digestive capacity and increased range of items included in the diet. These factors combined to ensure that energy intake matched an individual's requirements for all but one month of the year. Therefore if herbivores can coincide their breeding season with the time of maximum available food, and compensate for times of food shortage through changes in behaviour and physiology (for example using fat stores), thereby resulting in neither a reduced reproductive output, or increased mortality, the population need not be food limited, even in a seasonal environment.

However, simple food limitation may be confounded by complicated interactions with behaviour and predation. For example, the social behaviour of snowshoe hares (*Lepus americanus*) determines which individuals will suffer from food shortage: those animals lower down the social scale tend to suffer most when food is limiting, whereas dominant animals may not suffer at all (Sinclair 1986). Under such circumstances, behaviour has an influence on survival and therefore population size by causing the death of animals that might have survived if food resources were shared equally. This leads to the hypothesis that it is not a single factor which limits a population, but a combination of factors: the multi-factor population limitation hypothesis (Sinclair 1986). This hypothesis states that a combination of factors limit a population at any one time.

Predators and parasites are known to be more likely to affect nutritionally weakened animals. Serengeti wildebeest (*Connochaetes taurinus*) are known to be at greater risks of predation and disease if they are in poor body condition (Sinclair 1977; Sinclair & Arcese 1995). In this way, disease and predators interact with food availability to limit (and regulate) wildebeest populations. Therefore, the interaction between predators, disease and food supply will critically depend on the level of food resources. Complicating these interactions further, animals may increase their predation risk to decrease the chance of starvation, thereby affecting the balance of predation and starvation (Krebs & Kacelnik 1991).

McNamara & Houston (1987) created a relatively simple model of the starvation - predation trade-off, where an animal reduces its risk of starvation by increasing its chance of predation. Under such circumstances, the optimal strategy will be one which minimises total mortality. In the model, the effects on starvation and predation rate are examined under different conditions of environmental harshness (different temperature) and lowered food availability. The model showed that in certain circumstances, the rate of starvation may lower with decreasing food availability, and with increasing environmental harshness - as animals increase their predation risk to decrease the chance of starvation - i.e. predators kill animals before they starve. Therefore, lowered food availability can increase predation risk both by weakening the animal and by making it increase its predation risk. This work also suggests that low levels of starvation in a population does not necessarily mean that the animals in the population are not in danger of starving, or that food is not one of the major limiting factors for a population.

It is clear that the study of population limitation is neither simple or straightforward. To gain a full understanding of the relationships between a population and its limiting factors requires extensive research, often involving large scale, long term experiments (Sinclair 1986). For most studies, the problem must be simplified and properly defined, so that the results can be properly interpreted. It is possible to determine if a herbivore population is resource limited, but it is important to realise that other complicated interactions may also be occurring, which have important consequences for determining the abundance of a species. This does not mean that determining whether or not a species is resource limited is unimportant: it means that it is an important part of a much larger question.

1.3 The study of herbivores and resources: determining resource limitation

Critical to understanding the relationship between herbivores and resources is the changing pattern of resource availability and requirements through the course of the year. The first step is to determine the basic population statistics of the species: density, sex ratio, life table structure and reproduction. On this basis, the resource requirements of individuals at different times can be assessed. In order to determine the resources available, field studies measuring productivity and quality of food can be carried out, and the diet predicted. However, a much more powerful approach is to let the animal select the food from its environment and measure directly the quality and quantity obtained and match the rate of intake of food with demand, normally in terms of energy or nutrient intake.

Estimating the energy and nutrients obtained from a particular diet is of particular concern in animal husbandry and has been the subject of a great deal of

research, much of which applies to studies on wild herbivores (e.g. see Van Soest 1994). The nutrient and energy exchange which occurs during the process of digestion can be determined, and from that so can the resulting energy and nutrients which are available for the animal to use for maintenance, growth and reproduction. If a population of herbivores is resource limited, the energy and/or nutrients available to the animal will not meet the demands at a critical time. It is therefore possible that the rate of exchange of energy and nutrients may be limiting, rather than a straightforward shortage. If a population is limited in this manner, the resource need not be completely used up. For example, a herbivore population may be limited by the rate at which it can obtain energy from its diet, rather than a lack of diet. In this case, digestible energy will then be the limiting resource, and if it is increased in the diet, the population will increase.

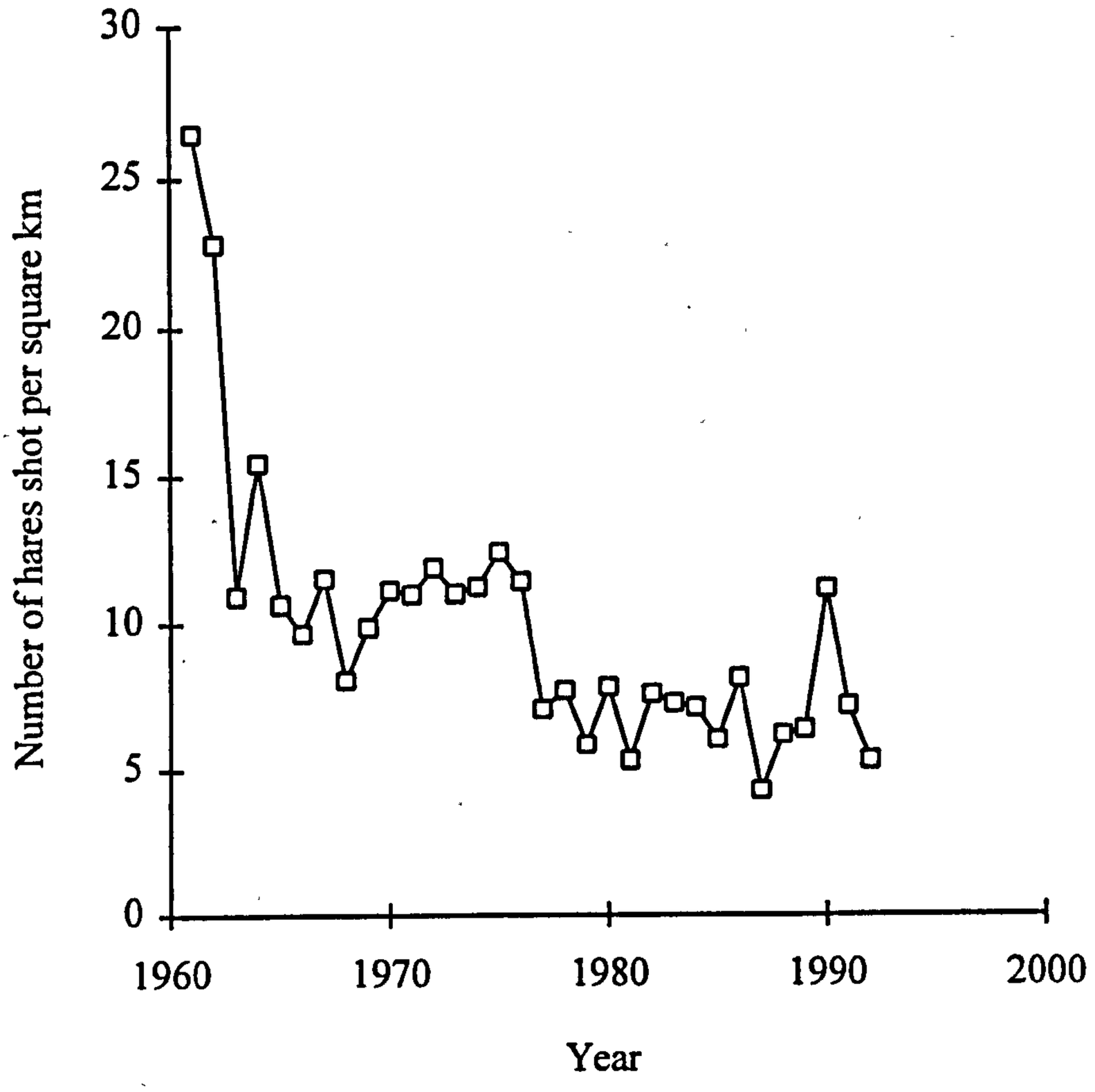
Controlled experiments which manipulate the level of resources are the next step in understanding the process of limitation. For example, if food is limiting a population, then the addition of abundant, high quality food would result in increased density. Sinclair *et al.* (1988) supplemented the diet of snowshoe hares, a species which undergoes ten year cycles of abundance. In the experimental areas, high quality food was added, but this failed to prevent a population crash. The conclusion drawn was that simple food availability was not the cause of the ten year hare-abundance cycle. Similar results were found in prarie voles (*Microtus ochrogaster*), another species which exhibits cyclical changes of abundance (Cole & Batzli 1978). Despite the voles reaching higher densities and having better survival chances where extra food was given, the treated populations still crashed at the same time as

surrounding control populations. Thus, food availability was found to determine the amplitude of the cyclical changes, but not the frequency. Both these cases demonstrate the importance of experiments in the study of population limitation and the possible complexity involved. However, as the numbers of variables increase, for example, to include predator removal, so must the scale of the experiments.

1.4 Herbivores and resources: the case of the brown hare

In Great Britain and most of Europe, brown hares (*Lepus europaeus*) have undergone a widespread decline in number (Tapper & Barnes 1986). Since the early 1960s national game bag figures have shown that the average number of hares shot per km^2 has declined throughout the country, (Tapper & Parsons 1986). Figure 1.1 shows the data for the East Anglia region, where there was the typical pattern of the decline: a crash in the 1960s followed by slow decline and possible stability by the late 1980s. Game bag data prior to 1961 is more scarce, but the available data suggests that hare populaions were much higher in East Anglia and the rest of the country prior to the 1960s (Hutchings & Harris 1996). A recent survey found that in Great Britain, hares were almost entirely confined to arable (crop producing) areas (Hutchings & Harris 1996), where they feed largely on crops and use woods and hedges as lying up sites whilst not feeding (Tapper & Barnes 1986). Although there is a good deal of information on hare population dynamics and behaviour (e.g. Andersen 1957; Broekhuizen & Maaskamp 1981; Frylestam 1980; Wasilewski 1991), the question of what limits brown hare numbers, and thus caused the decline of hare populations, has still not been resolved. The problem remains that although agricultural

Figure 1.1. The decline of brown hare populations in East Anglia, based on the numbers of hares killed in the February shoots, redrawn from Tapper & Parsons (1984). Data of this type have been collected by the U.K. Game conservancy each year since 1961 (Tapper & Parsons 1984).



intensification is frequently cited as the cause of the hare's decline, hares remain abundant in many arable areas (Flux & Angermann 1990; Hutchings & Harris 1996).

Brown hare populations are characterised by rapid turnover i.e. high adult mortality and high recruitment rates. Studies therefore tend to concentrate on the mortality and productivity of hare populations, since the factors which govern these two parameters will be the most important in determining population size.

Both fecundity and mortality rates vary between studies (Frylestam 1980; Broekhuizen 1979; Broekhuizen & Maaskamp 1981) and this leads to variation in density (Frylestam 1980). Also, the mean litter size at a given site is negatively related to the mean annual temperature of that site (Flux 1967). However, the number of offspring produced each year by a female tends to be similar between countries; where the breeding season is short, one or two large litters are produced, where it is longer, there is a tendency to produce several, smaller litters (Flux & Angermann 1990). As a result, a female tends to produce an average of about ten offspring per year (Flux & Angermann 1990).

Studies on hares have also found that the interval between subsequent litters can be shorter than the typical gestation length of 40 days, suggesting that fecundity can be increased by initiation and development of a new pregnancy in an already pregnant female, a phenomenon known as superfoetation, (Flux 1979; Broekhuizen & Maaskamp 1981; Stavy & Terkel 1992). This is rare in most other mammals, and although recorded regularly in captive hares, seems to be rare in free living hare populations (Flux 1979; Broekhuizen & Maaskamp 1981). Stavy & Terkel (1992) suggest that in many cases, the observed short interval between successive litters may

be the result of copulation in late pregnancy, which terminates the current pregnancy resulting in early birth and a new post-partum oestrus. Female hares also have the ability to store sperm for forty days (Flux 1979), meaning that one insemination could cover two pregnancies. These adaptations ensure that the interval between pregnancies is minimised, thus maximising female reproductive output.

Undoubtedly, the flexibility of the breeding strategy has allowed brown hares to be a successful coloniser of many countries, after introduction by man, and also to have a large natural range that covers most of Europe and eastwards into central Russia.

However, it is also known that hares are sensitive to changes in habitat; for example, Frylestam (1980) found that hares in areas of low landscape diversity had increased mortality, lower body weights and, as a result, produced fewer offspring. Tapper & Barnes (1986) radio-tracked hares and found that they used a succession of crop and grass types, preferring short cereals and grass, and avoiding them as they matured. Thus a diversity of crop types is important to ensure a year round supply of food for hares, and to maintain their high productivity. Arable regions throughout Europe have undergone a phase of rapid intensification since 1960, involving an increased use of pesticides and fertilisers, an increase in field size as a result of the removal of woodland and hedgerow, and an increase in specialisation towards particular crop types (O'Connor & Shrubb 1986; Britton 1990).

Clearly, hare populations are sensitive to changes in habitat structure, and are highly likely to have been affected by agricultural intensification. However, hares are also flexible in terms of reproductive output, across a wide range of conditions. Understanding the relationship between habitat and hare population dynamics is

therefore crucial in understanding the way in which hare populations are limited.

Brown hares therefore represent an ideal model for studying resource limitation, since: (i) the dramatic decline in numbers may mean that the limiting factor(s) are very obvious; (ii) there is a good deal of published information on the ecology and behaviour of hares; (iii) hares are shot in large numbers every February in Great Britain providing samples for post-mortem and population analysis; (iv) the changes in the arable environment have been documented by the Ministry of Agriculture, Fisheries and Food, in the form of the annual June farming census, providing valuable information on the changing food availability for hares; (v) arable environments are relatively simple, being dominated by only a few crop types, making the analysis of food availability much easier.

1.5 Thesis aims and structure

The aim of this thesis is to test the hypothesis that hares are food-resource limited in the modern arable ecosystem, and that this has been brought about by habitat change which has occurred over the past thirty years. This hypothesis makes four critical predictions which will be tested in the following chapters: (i) brown hare density will be related to the presence of habitat features which act as food resources; (ii) at a critical time of the year, the available food resources will not match the requirements of hares; (iii) at this critical time, there will be changes to the birth and/or death rates of the hare population which act to limit the size of the population; (iv) hare populations were not limited in this way prior to the decline.

In chapters two and three the population dynamics of brown hares are examined, in order to test predictions (i) and (ii) above. Comparative population data

from the 1960s, 1970s and the 1990s are used to examine the changes that have occurred during the decline in hare numbers, and these are related to changes in agricultural practice, testing predictions (iii) and (iv). A model hare population is created using a computer package, to determine the sensitivity of hare populations to changes in population dynamics, and also to simulate the decline of hare populations since 1960.

Chapter four tests predictions (ii) and (iii) further. This is done by determining the nutritional requirements of hares and matching this with the actual nutritional balance of hares observed at different times of the year.

Chapter five gives a general discussion of the results, and the implications for the general theory of population limitation. Further research strategies are also considered, which would shed light on the interactions between food, predators and disease in hare populations.

1.6 Summary

(1) Animal populations have the capacity to increase exponentially. The study of animal abundance aims to understand what limits and controls this capacity.

(2) Initial work led to two main theories: density dependence and environmental harshness. The crucial difference between the two theories was the idea that populations fluctuated around an equilibrium density, as a result of regulatory processes.

(3) Early debate was clouded by misunderstandings of the terms regulation and limitation. Regulation is the process by which a population returns to an equilibrium density, limitation is the process that sets the equilibrium density.

(4) Populations can be limited by many different factors, which may vary in the strength of their actions: any factor which removes members of the population is a limiting factor.

(5) Herbivore populations were initially thought not to be limited by food, since the amount of food eaten by herbivores is typically less than 10% of primary production. However, studies have shown that food availability varies seasonally, and that in some herbivore populations, individuals may be food limited at times when food is in short supply.

(6) Determining the pattern of food requirements and food availability throughout the year is therefore critical to understanding if herbivores are food limited.

(7) Brown hares represent an ideal study animal for examining food limitation, since their biology and ecology have been well documented. In addition, they have declined in abundance over recent years as the arable environment they inhabit has changed. The hypothesis tested in this thesis is that habitat change has reduced hare numbers through food limitation.

CHAPTER TWO

THE POPULATION DYNAMICS OF BROWN HARES: THE ROLE OF AGRICULTURAL INTENSIFICATION

2.1 Introduction

A detailed knowledge of population dynamics is crucial in understanding the way in which a population is limited. Key components of population dynamics are the patterns of fecundity and survivorship of individuals. Clearly, if periods of low survivorship or fecundity can be identified, these are likely to be key times for the population, and are likely to limit that population.

For a population that has undergone a decline a comparison of the population at high and low densities should help identify the factors which result in the limitation of the lower density population. For example, lapwings (*Vanellus vanellus*) have undergone a steady decline in arable areas since 1962. Surveys by the British Trust for Ornithology found that lapwings nested preferentially on spring tillage (land that is ploughed and cultivated annually), but then moved their chicks to grassland areas for feeding (O'Connor & Shrubb 1986). In modern arable areas, lapwings increasingly used tilled land to feed their chicks as the area of grassland declined, resulting in a much lower chick survival (O'Connor & Shrubb 1986). In addition, the introduction of fertilisers, herbicides and new crop varieties changed the structure of cereal crops, making them more dense, and much more even. This greatly decreased the number of sparse patches of crop in which the birds preferred to breed, and reduced nest density (O'Connor & Shrubb 1986). Thus the populations

are limited by a lack of nesting sites and poor chick survival. However, detailed information of this type is not available for most species. Fortunately, data on brown hare populations are available from studies carried out in Great Britain in the 1960s and 1970s (Lloyd 1968; Lincoln 1974; Hewson & Taylor 1975; G. Lincoln, unpublished data). Unfortunately, there are no data on UK hare populations prior to the 1960s decline. However, data were available from a study in New Zealand from 1960 to 1963 in which hares were considered to be at pest densities (Flux 1967). A direct comparison of the data from Flux (1967) and Lincoln (1974) reveals a very similar pattern of productivity (overall leveret production): breeding starting in winter, and overall leveret production reaching a peak in summer and tailing off towards the end of the year (Table 2.1). The breeding season in New Zealand was longer, but the overall fecundity of the females was similar at between nine and ten offspring per year (Table 2.1), and this is the typical number of offspring produced by hares each year (Flux 1967). As a result of the similarity and overall high fecundity of the hares in the 1970s samples (Lloyd 1968; Lincoln 1974; Hewson & Taylor 1976; Table 2.1), it is used in this chapter as if the fecundity values were comparable to pre-decline data. This finding is also important as it implies that it was not changes in fecundity which led to the decline of hare populations.

The aim of this chapter therefore, is to obtain data on the population dynamics of 1990s hare populations, so that these can be compared with previous studies, and also used to highlight the important factors which influence present day hare densities. This information is combined with detailed information on habitat change and hare abundance over the past thirty years. In this way, the changes that

Table 2.1 A comparison of breeding data for brown hare populations

	East Anglia 1971[a]		New Zealand 1960[b]		Scotland 1960/61[c]	
Month	litter size	% pregnant	litter size	% pregnant	litter size	% pregnant
January	1.0	40	1.0	2	2.0	38
February	1.2	65	1.1	50	2.0	68
March	2.1	77	1.2	100	3.0	92
April	3.6	100	2.3	100	3.3	100
May	3.6	100	2.5	90	3.5	100
June	3.2	100	2.8	100	2.2	62
July	2.8	100	2.6	95	2.0	62
August	1.0	59	2.8	95	2.0	62
September	0.0	0	2.3	95	2.0	62
October	0.0	0	2.7	15	2.0	30
November	0.0	0	2.0	8	0.0	0
December	0.0	0	0.0	0	0.0	0
Mean fecundity† per female	9.7		10.7		10.0	

a: data from Lincon (1974)

b: data from Flux 1967. The breeding season in New Zealand starts in June. For clarity and comparability in the table above, the New Zealand data has been rescaled so that breeding starts in January

c: data from Hewson & Taylor (1975)

†calculated as Σ ((litter size× % pregnant)/geatation length ×100); see methods and Broekhuizen & Maaskamp (1984) Gestation length is given as 1.6 (see section 2.2.5).

have occurred in hare populations will be directly related to habitat change. Critically, the role that habitats, such as woodland, hedge and arable, have in determining the abundance of present day hare populations will be examined, to critically test the hypothesis that habitat change has been detrimental to hare populations.

2.2 Methods

2.2.1 The study areas and collection of samples

Six arable farming estates in East Anglia were chosen for the study (Figure 2.1). The six study areas were typical of arable areas of East Anglia, in February: a mixture of winter cereals (mostly wheat), oilseed rape, plough (includes fields with non-emerged winter beans), stubble and set-aside, (areas left uncultivated on a one year rotation basis - there was no permanent set-aside on any of the study areas). There were also small areas of improved grassland, linear features (hedgerows, ditches and embankments) and woodland. In addition, there were woodland strips and areas of other cover (mostly maize) planted for game cover. Other non-arable features (e.g. roads, streams and houses) constituted only a small fraction on any of the study areas. Other crops, typical of the area, were either just beginning to emerge in February (winter beans), or had yet to be planted (sugar beet, cabbage, onions and potatoes). Comparable data were available for the region from the 1960s and 1970s (Lloyd 1967; Lincoln 1974; G. Lincoln unpublished data). The region has undergone widespread agricultural intensification, and suffered a 75% decline in hare numbers since 1961 (Tapper & Barnes 1986). Despite this, hare densities remain

high enough for a sample to be obtained from annually organised shoots. Also, by examining a number of sites over a relatively small area, any effect of weather variation between sites was minimised, and since all sites were managed by at least one gamekeeper, so were the effects of predator control (Tapper, Potts & Brockless 1991).

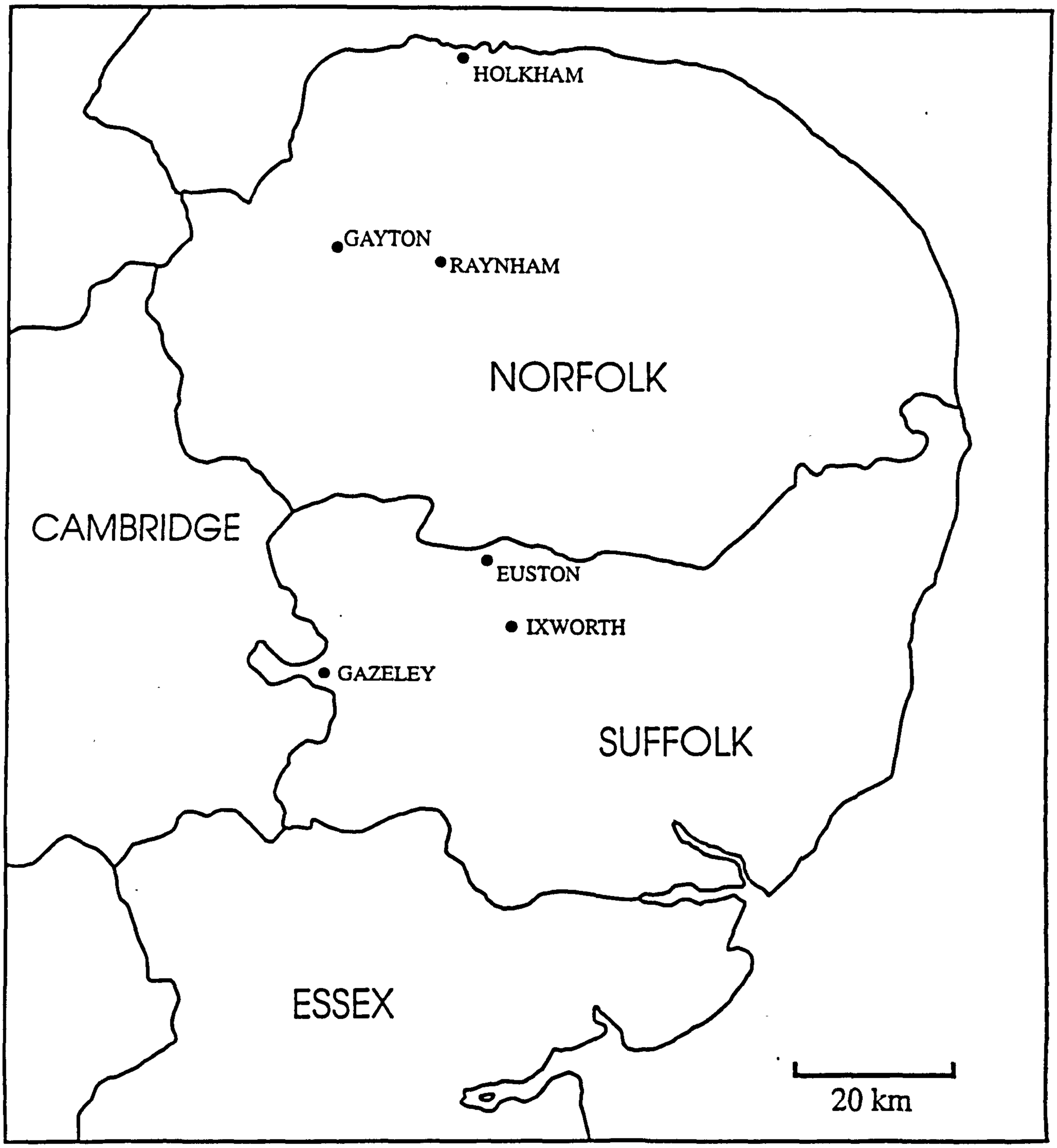
All six study areas organise annual driven hare shoots (Figure 2.1), which occur on one day, normally within the first two weeks of February. These involve surrounding an area with guns on all sides, one side remaining standing while the others walk towards the standing guns, thus flushing the hares out of their resting sites. Driven hare shoots are a non-selective form of hunting, in that virtually all the flushed hares will be shot (Pepin 1987). However, leverets will be missed in this form of sampling, since they do not flush from cover (Sargent 1974).

All the samples were collected between the sixth and the thirteenth of February 1993. Up to the first 100 hares from each shoot were taken. This provided samples that were directly comparable between sites, since all the samples were shot within a few days of each other and at the same time of day, thus removing the effects of any annual or circadian differences between sites.

2.2.2 The post-mortem analysis

Each carcass was weighed to the nearest 0.01 kg (body weight) and measured from the tip of the nose to the base of the tail to the nearest 1 mm (body length). The length of the hind foot was also measured from the tip of the longest digit to the opposite end of the foot in to the nearest 1 mm (hind foot length). After recording the number of visible foetuses, the stomach, intestines and reproductive tract were

Figure 2.1 Map of the study areas



removed, and the animal was re-weighed to the nearest 0.01 kg (carcass weight). Stomachs were weighed full and empty to the nearest 0.1 g to give an index of food intake, and the contents stored frozen. For males the paired testes and paired epididymides were both weighed to the nearest 0.1 g. From each animal both eye lenses and one lower jaw were removed for age determination. Lactating animals were identified on the basis of the exudation of milk from cut mammary tissue. Animals were given a kidney fat score from zero to five (full coverage of kidney by fat), as an index of condition.

2.2.3 Estimating population density and potential leveret production

Densities of hares were calculated by dividing the number of hares shot by the area over which they were shot, and therefore represented a minimum population estimate. Potential leveret production for February was calculated by determining the total number of visible foetuses per km^2 at the time of the shoot. Thus it is an index of breeding potential at the time of the shoot, rather than an absolute estimate of the actual February productivity.

2.2.4 Estimating the age of the animals

Initially, each animal was given an age in days, based on the dry weight of the eye lens. Eye lenses were removed and dried at 100°C for 24 hours, and ages were then based on the growth curve produced by Suchentrunk, Willing & Hartl (1991). The lenses were taken straight from the animal to the drying oven, thus avoiding the need to take freezing or prolonged storage into account (Suchentrunk, Willing & Hartl 1991). Eye lens weight can reasonably estimate age in days for animals up to 450

days old i.e. for this study it was adequate to cover all the previous year's births. In this way, all the animals born in 1992 were assigned to a month of birth.

For animals born before 1992, age in years was estimated using periosteal growth lines in the lower jaw. Jaw sections were decalcified in 10% nitric acid for between 24 and 48 hours, and transverse sections approximately 20 micrometers thick cut on a freezing microtome from the region of the jaw below the molars (Frylestam & von Schantz 1977). The sections were stained in a 10% solution of toluidiene-blue for 5 minutes, mounted in glycerol and examined by light microscope. The interpretation of the sections was as described by Frylestam & von Schantz (1977).

2.2.5 Estimating survivorship

Survivorship is defined as the proportion of individuals which persist per unit time (Caughley 1977). Estimating survivorship is fraught with difficulty, although it is crucial to understanding population dynamics (Krebs 1989). For animals aged one year and over, an estimate of survivorship from one year to the next can be calculated, for an animal aged n years, by dividing the number of animals aged n+1 by the number aged n (Caughley 1977). Estimating the survivorship of animals under one year is more complex, since the number of offspring born must be known. These data were not available. However, since the eye lens data aged animals to a month of birth, it was possible to calculate the monthly pattern of survivorship of leverets through the year. To do this, for each month in 1992, the number of leverets which survived to the February 1993 shoot was divided by the estimated number born in that month. The number of animals born in each month was estimated using

data collected in East Anglia in the early 1970s on monthly pregnancy rates and litter size (Lincoln 1974; Table 2.1) and the formula given by Broekhuizen & Maaskamp (1981):

$$n = \% \text{ pregnant females} \times \text{litter size} / (\text{gestation length} \times 100)$$

where n= the number of births. By this means, an expected monthly productivity was calculated for a total population of 288 females (the total number in the February 1993 sample), and for each estate by using the number of females in each sample. Then, assuming a constant population, the number of animals who were aged to a particular month were divided by the estimated number of births in that month. In this way, the survivorship value of each month indicates the chance of surviving to the next February, not for a year, or to reach adulthood. In theory, the survivorship value should increase steadily as the birth date approaches the end of the year, and any variation in this will identify periods of greater leveret mortality or survival. Clearly, this measure of survivorship is only a rough estimate and care must be taken in its interpretation. Most importantly, it assumes that the number of leverets born each month has remained the same since the sample collected by Lincoln (1974), when hare populations in the area were higher (Tapper & Parsons 1984). If this was not the case, the estimate of survivorship in the 1993 sample may therefore reflect changes in fecundity as well as true leveret survivorship.

To calculate mean leveret survivorship, the expected fecundity for each month was multiplied by the expected survivorship of that month. This gives the total number of leverets which survive, and this is divided by the total fecundity to give overall mean leveret survivorship.

2.2.6 Habitat diversity and management of each estate

Each estate was asked to complete a questionnaire, giving details of the shooting and habitat management regimes, including set-aside and game management strategies, for the area from which the sample was obtained. Each estate was also asked how the 1993 hare bag compared to that of previous years, and comparative figures were supplied. Thus it was known for each estate whether 1993 had been unusual in any way.

For the area sampled on each estate, the areas of crop, set-aside, woodland, linear and any other features were measured either in the field, or from maps using a bit-pad.

2.2.7 Diet analysis

The species composition of food in the stomach was determined. The stomachs were first divided into estate categories, then males and females. Samples of stomach contents were then filtered on a 80 μm sieve to remove very small non-identifiable fragments. Samples were then placed on a microscope slide and spread evenly in glycerol. The fragments were then observed at ×40 magnification and identified using a key for plants to the region (Forde 1989). Ten transects were then taken across each slide and the area of each plant fragment measured using an eyepiece graticule. For each category, 10 slides were measured.

2.2.8 Hare population data from the 1970s

Data from February hare culls in East Anglia in 1972, 1974 and 1975 were used as a comparable data set (Lincoln 1974; G. Lincoln unpublished data). These data consist

of age structures based on the eye lens weight of the shot animals: other unpublished data were not available. Some of these data has been published, in conjunction with data on hare reproduction throughout the year (Lincoln 1974; see Tables 2.1 & 2.2). The method of collecting and analysing the 1970s data is very similar to that used here, and is fully described by Lincoln (1974). Most of the 1970s cull data were taken from one site, and the shoots were held over two days, and in 1972, 1974 and 1975, and the total hare bag exceeded 1000 animals in each year (Lincoln G. *pers comm*). Thus these hare shoots killed far more hares than in 1993, although the area of the shoot is not known so density comparisons cannot be carried out. By 1970 however, much of the hare decline had taken place (Tapper & France 1992), and these data may reflect a population that was limited in a similar manner as the 1993 sample. To examine this, the age structure of the 1970s populations were determined, as was leveret survivorship, which is estimated by the method described above in section 2.2.5.

2.2.9 Habitat change from 1961 to 1992

For each year from 1961-1992 (the same period for which game bag data from East Anglia were available), the area of cereals, grasses, sugar beet , oilseed rape and other crops were available from the Ministry of Agriculture Fisheries & Food (MAFF) annual June census (MAFF 1961-1992). However, not all details are recorded in the MAFF census, and one significant omission in the records prior to 1979 is the timing of planting of cereals. This is of great importance to hares, as this determines when hares will feed on them (Tapper & Barnes 1986). Therefore, prior to 1979 the area of winter and spring cereals in East Anglia was estimated using

Table 2.2 The 1970s post-mortem data, supplied by G. Lincoln, *pers. comm.* and also from Lincoln (1974). The data were taken from February culls in the East Anglia region in the year specified. Most of the animals were shot at one site, but the data from 1972, includes animals shot on three other sites in East Anglia.

	Year collected		
	1972	1974	1975
Number of hares post-mortemed	550	408	463
% Males	49.6	50.7	44.9
% Females	50.4	49.3	55.1
% of animals over one year	26.8	38.0	36.1
% of animals under one year	73.2	62.0	63.9

national seed sale records, which record the percentage of winter and spring cereal seed sales (Britton 1990). The majority of the hares' diet in most arable areas is grass (Frylestam 1986), and therefore I decided to calculate the diversity of grass species available to hares during the period 1961-1992. The grass species included winter and spring cereals, ley grass (grass under five years old), permanent grassland and rough grazing. The Simpsons diversity index (Magurran 1990) was then calculated for each year. The change in area of the major crop types in the region since 1961 were also calculated

2.2.10 Statistical analyses

For normally distributed data, parametric tests were used throughout (ANOVA, t-test, correlation and regression). When data were non-parametric, Kruskal-Wallis, Chi ^{2}, Mann-Whitney U, and non-parametric correlation tests were used. Between study site variation was examined using ANOVA or Kruskal-Wallis tests. When the ANOVA procedure was carried out to examine between site variation, the Tukey-b test was used to examine significance. Within sample variation (e.g. between sexes) was examined using t- tests or Mann-Whitney U tests.

2.3 Results

2.3.1 The densities of hares in February 1993

The numbers and densities of hares shot in February 1993 on the six estates are summarised in Table 2.3. There was no evidence that 1993 was in any way exceptional, and hare densities in the six study areas where comparable to their recent bag records. The range of densities found was large, and it was therefore decided to

Table 2.3 Number of hares obtained for post-mortem analysis from each estate and the number of hares shot per km^2.

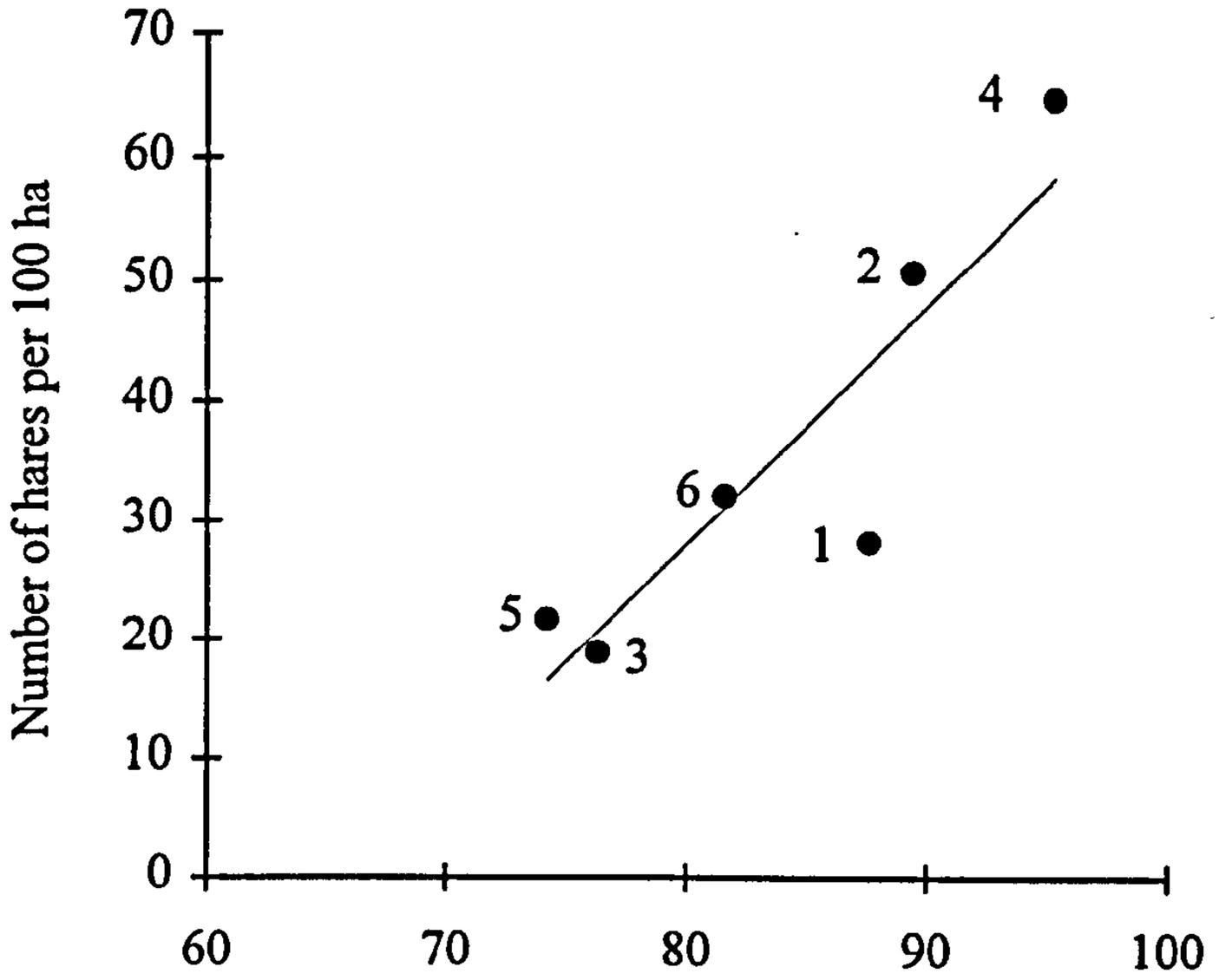
Estate	Number of hares shot/km^2	Area of shoot, km^2	Number obtained
Euston, Suffolk	28.3	3.46	100
Gayton, Suffolk	50.8	1.90	100
Gazeley, Norfolk	18.9	3.27	69
Holkam, Norfolk	64.8	2.40	100
Ixworth, Suffolk	21.8	5.08	98
Raynham, Norfolk	32.2	4.20	100

examine possible relationships between density and habitat, although the number of sites was low. To examine one of the major effects of agricultural intensification, that of the loss of habitats such as woodland and hedgerows to arable, density was regressed with the 'arable area': the combined area of winter cereals, plough, stubble and set-aside. This was not quite a statistically significant, positive relationship (R^2=0.76; ANOVA DF=1,4, F=4.1, p<0.07). While winter cereals, plough, set-aside and stubble may provide food (and shelter) for hares (Tapper & Barnes 1986), oilseed rape was not present in the diet (see section 2.3.6), and is known to be avoided by hares after about one month after sprouting, and at most is used as forage up until the beginning of December (Frylestam 1986). Therefore, oilseed rape was removed from the calculated arable area, and when regressed with density the relationship was significant (Figure 2.2 R^2=0.92, ANOVA DF=1,4, F=16.9, p<0.01). Thus there was no evidence that the expansion of arable has had a negative effect on hare populations: the data here suggest the opposite .

2.3.2 The condition and reproductive status of hares in relation to age, sex and habitat factors

In February females were significantly heavier than males for both body and carcass weights, although females did not have significantly longer body or hind foot lengths (Table 2.4). However, for males and females aged <200 days, there were no significant differences between the sexes for any body measurements (Table 2.4). An analysis of the between site variation showed no significant differences in either animals aged under or over 200 days (< 200 days, ANOVA DF = 5,118, F=0.58, N.S.; > 200 days ANOVA DF= 5,397 F= 2.0, N.S.).

Figure 2.2. The relationship between the density of hares on the six study areas and the area of winter cereal, plough, set-aside and stubble. The line is based on the regression equation between density and arable area, and this is given as: density=1.98 × arable area-130.



The sites are numbered in the graph above as follows: 1 Euston; 2 Gayton; 3 Gazeley; 4 Holkham; 5 Ixworth; 6 Raynham.

The difference in body weight of older animals was explained by growth equations based on carcass weights, which indicated that for males growth stops at about 200 days, but in females weight gain continues for a further 100 days, albeit at a much reduced rate (Table 2.5). It was also found that mean female carcass weight for fully grown females (>300 days old) was significantly and positively related with the area of winter cereals, plough, set-aside and stubble (Figure 2.3, R^2=0.94, ANOVA DF=1,4, F=9.1 p<0.01), the same factors that were related to population density. However, mean female adult weight was not significantly related to density (R^2=0.48, ANOVA DF=1,4, F=0.1 N.S.) suggesting that arable area has a direct influence on female body weight.

Table 2.6 summarises the reproductive data recorded for the different estates, with a comparison with data from the literature. The number of foetuses observed per female was positively correlated with carcass weight (Figure 2.4,n=288, r=0.04, p<0.001). This relationship was maintained when females <200 and >200 days were considered separately (animals <200 days, n=79, r=0.05, p<0.001; >200 days, n=209, r=0.04, p<0.001).

Both potential leveret production and mean male testis weight were found to be positively related with the proportion of the area covered in by winter cereals, plough, stubble and set-aside (potential productivity R^2=0.92, ANOVA DF=1,4, F=39.6 p<0.01, testis weight R^2=0.72, ANOVA DF=1,4, F=10.1 p<0.01), the same features which were found to be related to density and female body weight. As the productivity calculation uses density, this result may be due to the confounding effects of density, although, testis weight was not found to be significantly related to

Table 2.4. Body size measurements for male and female brown hares, all estates combined.

Animals over 200 days			
	males (n=195)	females (n=209)	* p
mean body weight - kg	3.33	3.58	<0.001
mean carcass weight - kg	2.94	3.15	<0.001
mean body length - cm	62.6	62.9	N.S.
mean hind foot length - mm	132.0	133.0	N.S.

Animals 200 days and under			
	males (n=83)	females (n=79)	* p
mean body weight - kg	3.10	3.31	N.S.
mean carcass weight - kg	2.72	2.89	N.S.
mean body length - cm	61.5	61.7	N.S.
mean hind foot length - mm	130.9	132.5	N.S.

* p values are given for t-tests between sexes for all body measurements.

Table 2.5 Growth equations of male, female and juvenile hares. These represent linear regressions of carcass weight with age in days. The significance was tested using one-way Anova.

Animals aged 35-200 days, regression equation of carcass weight on age in days:

(*sexes combined, n =162)

weight = 0.003 (age in days) + 2.37

Anova $p<0.0001$

Animals aged 201 - 300 days regression equation of carcass weight on age in days:

Males, n=195

weight = 0.008 (age in days) + 2.69

Anova N.S.

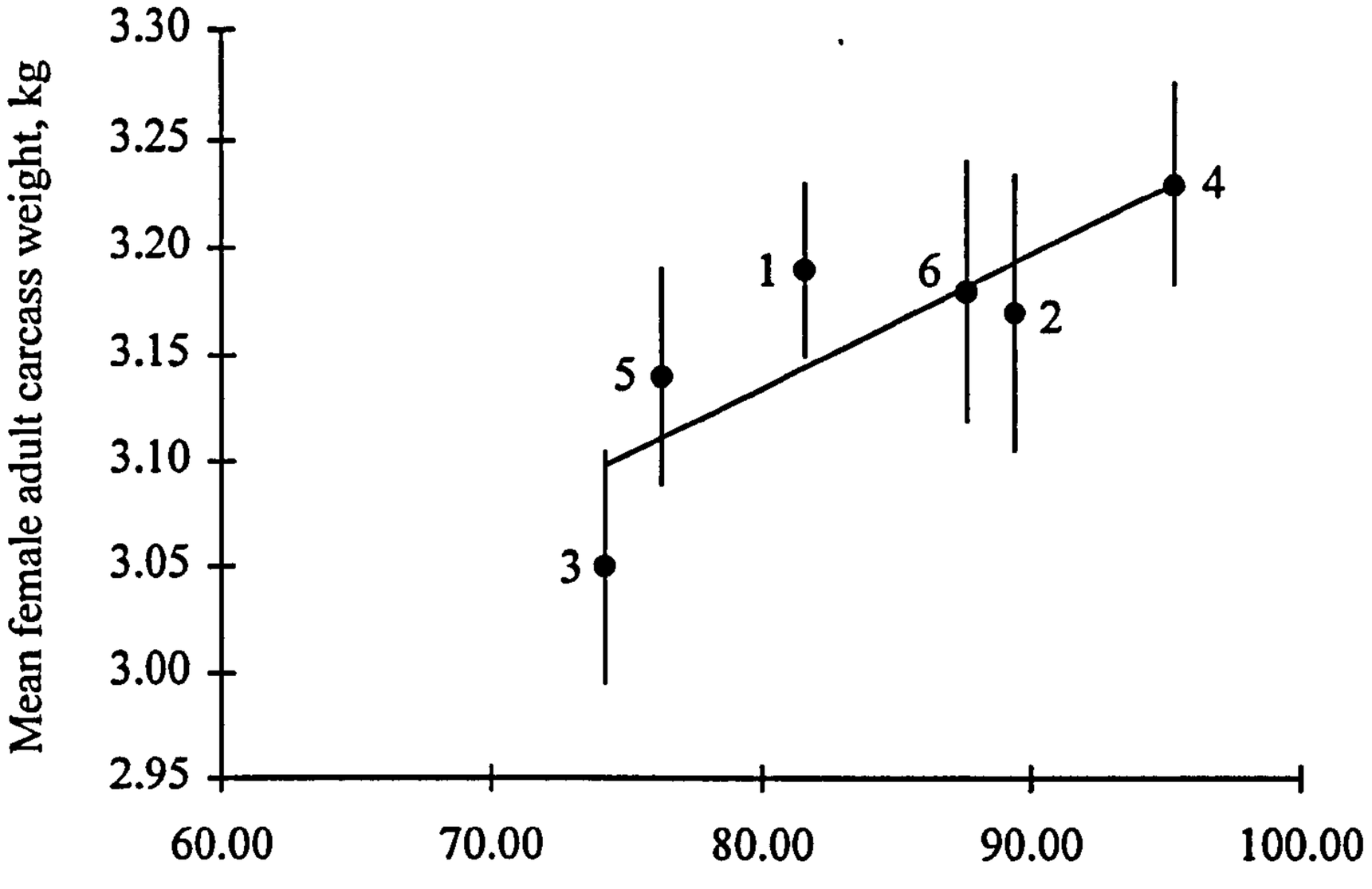
Females, n=209

weight = 0.002 (age in days) + 2.56

Anova $p<0.05$

* the sexes were combined because there were no significant differences for any of the body size measurements for animals under 200 days (see Table 2.4)

Figure 2.3 The relationship between mean female carcass weight (shown with one standard deviation) and the area of winter cereal, plough, set-aside and stubble. The x-axis in this figure is the same as that in Figure 2.2. The line is based on the regression equation which is given as: carcass weight=0.006×arable area+2.63.



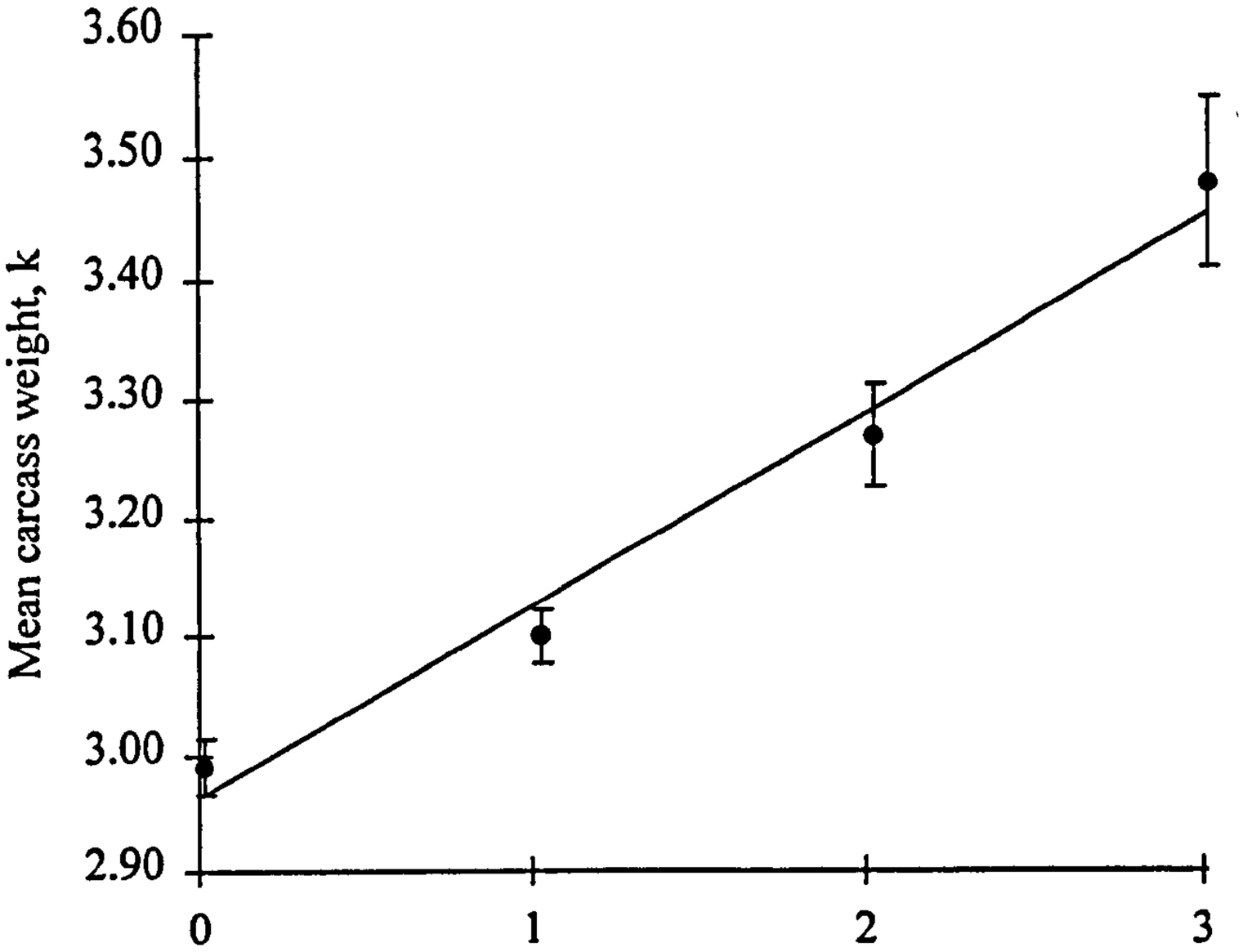
The sites are numbered in the graph above as follows: 1 Euston; 2 Gayton; 3 Gazeley; 4 Holkham; 5 Ixworth; 6 Raynham.

Table 2.6. A comparison of the reproductive status of female hares in February 1993 and February 1971/2

	Euston	Gayton	Gazeley	Holkam	Ixworth	Raynham	mean 1992	1971/2
sample size	47	50	25	58	55	53	-	13-20*
% of females with foetus	62	54	68	45	60	45	54	65
Mean number of foetuses per female	0.89	0.54	1.2	1.3	0.7	1.3	1.0	1.1
% lactating	0.0	0.0	4.0	8.6	9.4	0.0	3.7	0.0

* data from Lincoln (1974). Sample size for 1971/2 is estimated since only the range of the number of carcasses examined each month was given (13-20) for the two year study. The estimate assumes, therfore, that between twenty-six and forty animals were examined over two years and that half were female.

Figure 2.4 The relationship between the carcass weight of female hares (shown with the standard error), and the number of foetuses they were found to be carrying. The line is the regression equation, given as: carcass weight=0.16×number of foetus+2.96.



density (R^2=0.11, ANOVA DF=1,4, F=4.77, N.S.), suggesting that this was not the case. This suggests, that as with female body weight, there are direct influences of arable area on testis weight and potential productivity in hares. Therefore, where the proportion of winter cereals, plough, stubble and set- aside is greater, the density is greater, the females heavier and males have heavier testes; this results in increased productivity.

To determine if these effects were mediated by food availability, the difference in stomach weight between sites was examined, using oneway ANOVA. There was a significant difference in stomach content between sites, with Euston, Holkham and Raynham estates having a significantly higher stomach contents weight than the other sites (ANOVA DF=5, 560, F=17.3, p<0.0001. The sites with heavier stomach contents were those with lactating females and highest population density (see Tables 2.3 & 2.6). However, there was no relationship between the weight of the stomach contents and density (R^2=0.17, ANOVA DF=1,564, F=0.5, N.S.) or arable area (R^2=0.004, ANOVA DF=1,4, F=3.4 N.S.).

An analysis of the within sample variation showed that females had heavier stomachs than males (full and empty stomach weight), and mean full stomach weight of lactating females was approximately 50% greater than that of non-lactating females (Table 2.7). The presence of foetuses had no effect on stomach weight, full or empty. There was also significant variation between sites in kidney fat index (Kruskal - Wallis, n=565, p<0.05), although, the mean rank of kidney fat was not related with density (R^2=0.28, ANOVA DF=1,4, F=2.8, N.S.) or arable area (R^2=0.14, ANOVA DF=1,4, F=2.9 N.S.). Analysis of the within total sample

Table 2.7. The effects of sex on stomach weight full and empty.

	Stomach weight (g)	
	full	empty
All males	78.8 (n=267)	15.0 (n=97)
All females	86.0 (n=272)	15.9 (n=143)
**p^1	<0.001	<0.05
Reproductively inactive females*	86.6 (n=128)	15.7 (n=72)
Reproductively active females*	83.3 (n=131)	16.2 (n=71)
**p^2	>0.05	>0.05
Lactating females	118.0 (n=13)	15.6 (n=9)
**p^3	<0.001	>0.05

*Reproductively inactive females were defined as having no visible foetus; reproductively active females were those with at least one visible foetus.

** p values are for a two tailed t-test: p^1 males vs females; p^2 reproductively inactive females vs reproductively active females; p^3 Lactating females vs reproductively active females for both full and empty measurements.

variation showed that kidney fat index was significantly higher in females than males (Mann-Whitney U test, n=565, z=-4.1, $p<0.001$). Between breeding and non-breeding females there was no significant difference (Mann-Whitney U test, n=277, z=-1.73, N.S.), although, lactating females had a significantly lower kidney fat index than non-lactating females males (Mann-Whitney U test, n=143, z=-2.7, $p<0.01$).

The mean rank of kidney fat for the hares on an estate was found to be strongly correlated with the mean stomach contents weight found on that estate (non-parametric correlation, n=565, r=0.90, $p<0.05$).

The eye lens weight data and periosteal growth line data were combined to determine the time of the year in which the annuli in the periosteal bone become visible. Only 11 (17%) of the hares estimated to be between 350 and 400 days old i.e. animals born in the winter of 1991-1992, had a visible annulus. This suggests that annuli are not generally discernible from the outer edge of the jaw in February, and so one annulus was taken to indicate an animal entering its second year, two its third and so on. Using this as the basis on which to interpret the annuli, Table 2.8 shows the age structures of the hare samples from the six study areas.

2.3.3 Leveret production in 1992

The monthly leveret production for 1992, based on the eye lens data, is shown for the estates combined and for examples of three estates separately (Figure 2.5). The population density in February 1993 was positively related to the leveret production in the first two months of 1992 (Figure 2.6, $R^2=0.90$, ANOVA DF=1,4, F= 39.5 $p<0.01$), but not leveret production later in that year. The relative productivity from March onwards was positively and significantly related with the

Table 2.8. The age structures of the six study populations.

% of population in each age class

Estate	<1 yr	1-2 yrs	2-3 yrs	3-4 yrs	4-5 yrs
Euston	63.9	24.7	6.2	2.1	3.1
Gayton	76.0	16.7	6.3	1.0	-
Gazeley	81.8	16.7	1.5	-	-
Holkam	68.4	22.4	8.2	1.0	-
Ixworth	77.6	12.9	3.5	3.5	2.4
Raynham	55.8	27.4	9.5	6.3	1.1
Means	69.3	20.3	6.1	3.0	1.3
Survivorship	0.3	0.3	0.5	0.4	

Figure 2.5 The overall numbers of births which occurred during each month of 1992, based on the eye lens weight of all the hares shot in February 1993. Examples of three estates are also given in Figure 2.5a.

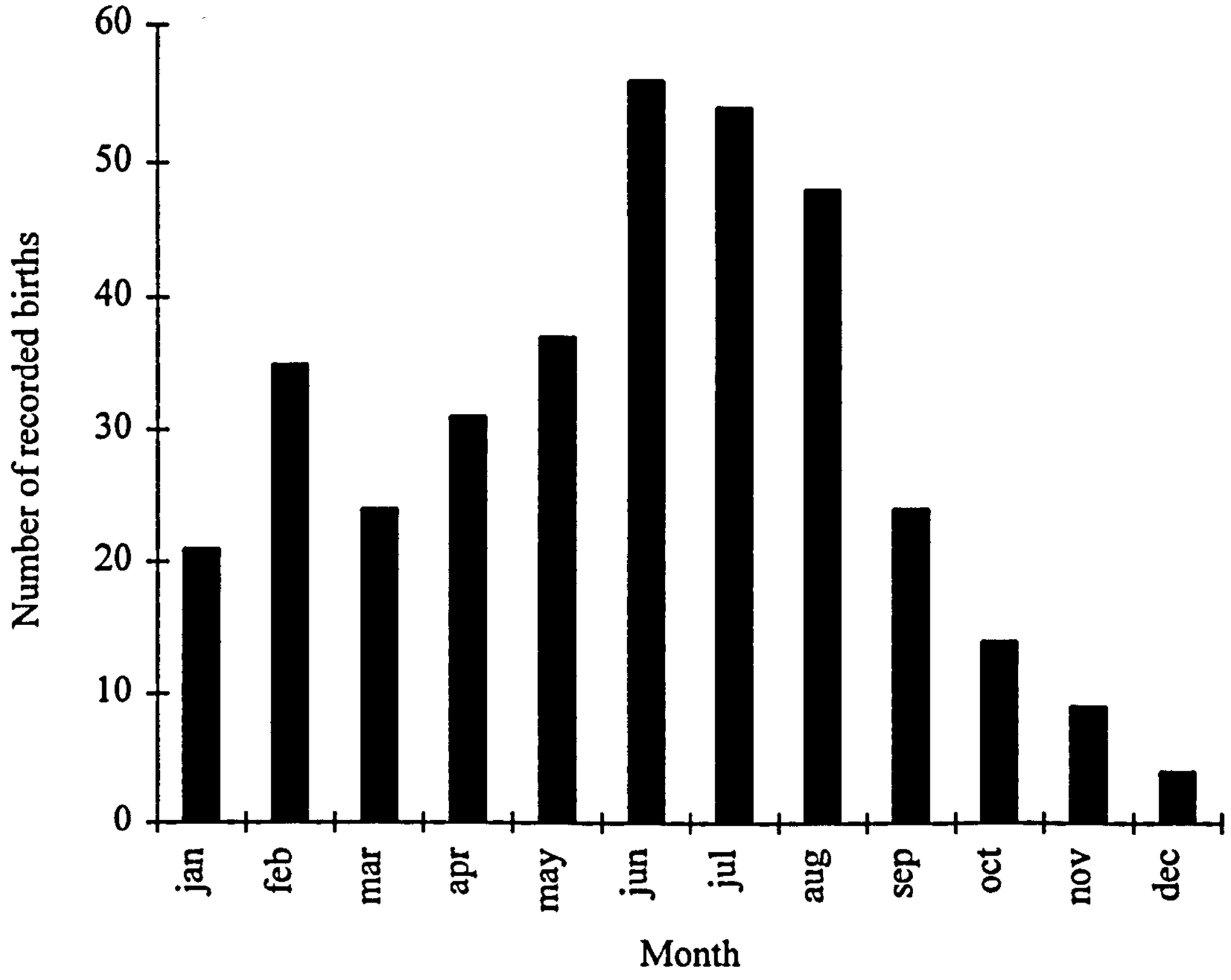
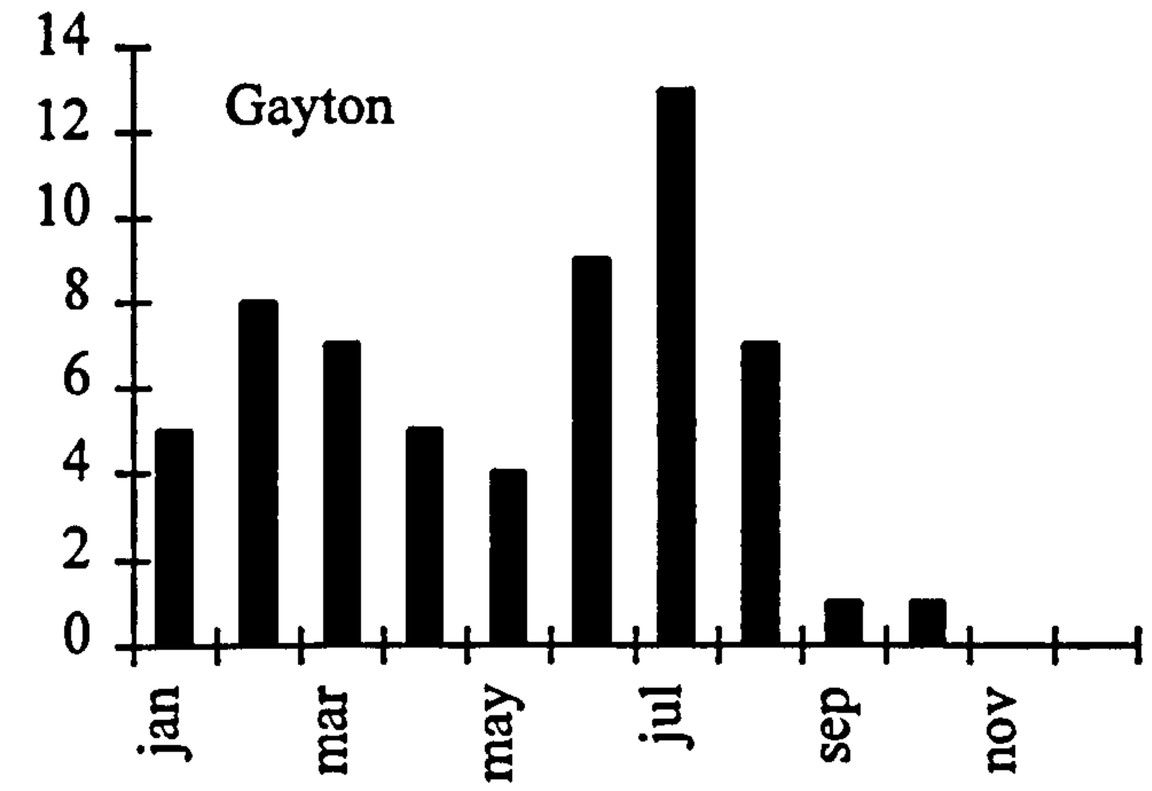
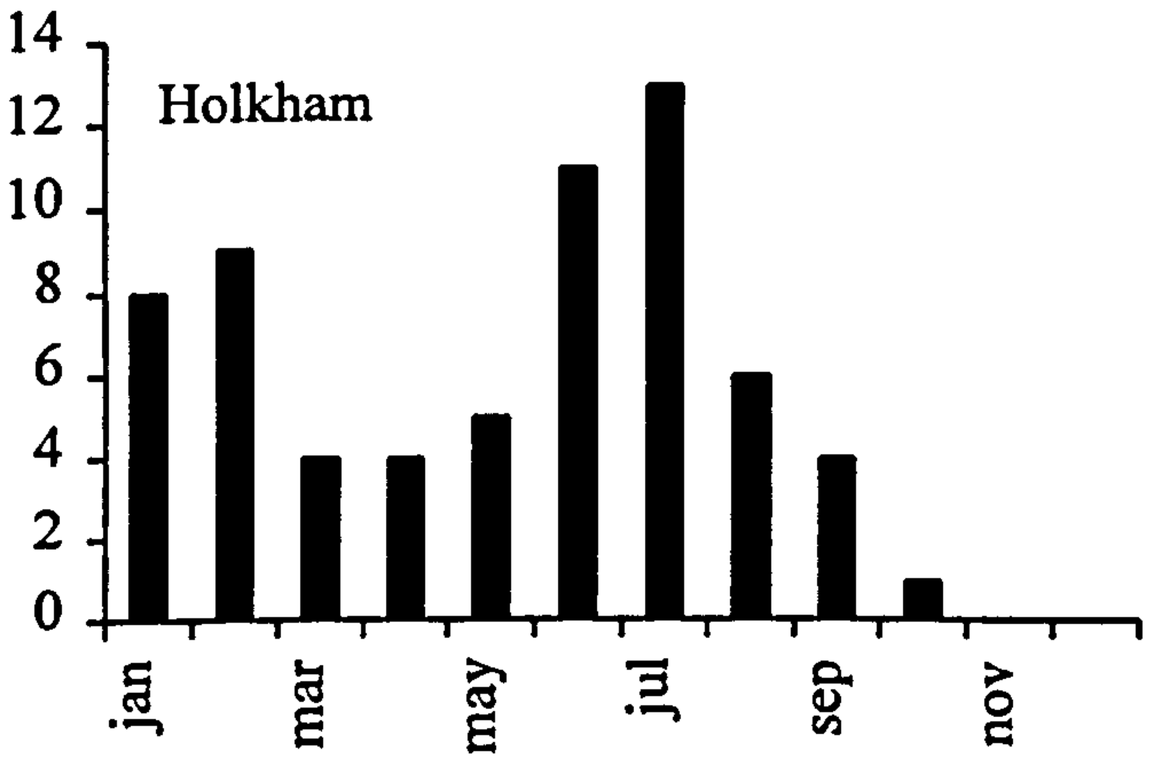


Figure 2.5a Examples of the age structures of three of the estates. All six estates showed similar patters.





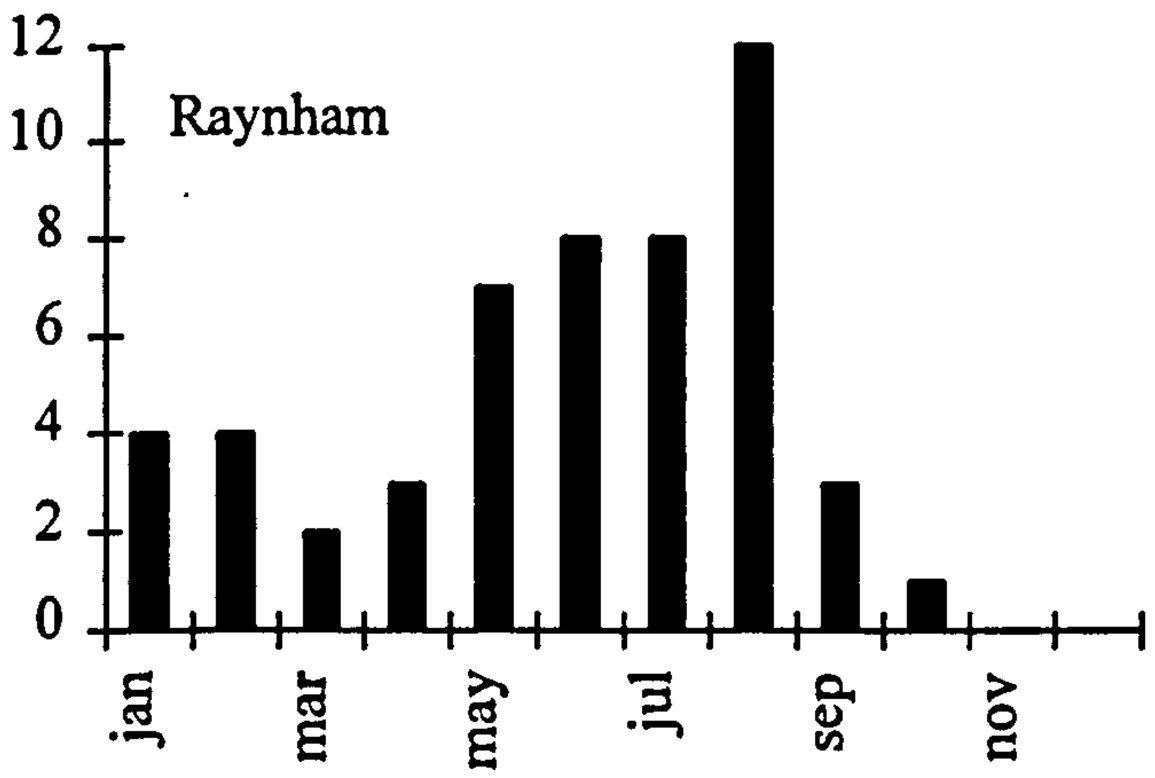
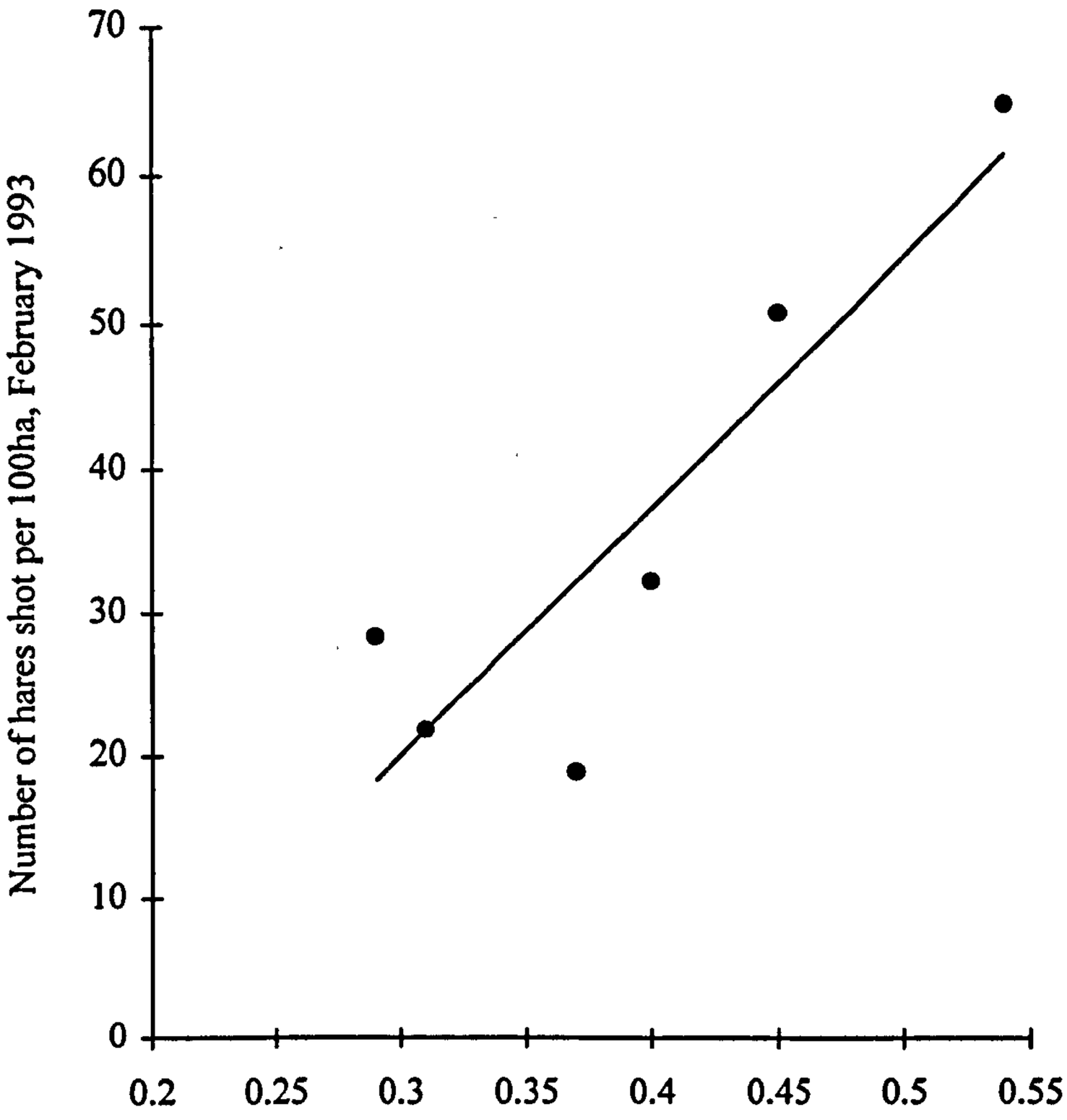


Figure 2.6 The relationship between the number of hares shot in February 1993 on the six study areas, with the proportion of births in 1992, that occurred in January and February. This shows that high density populations have a relatively greater investment in early breeding. The line is the regression equation, given as density=172.7×proportion of births-31.8.



The sites are numbered in the graph above as follows: 1 Euston; 2 Gayton; 3 Gazeley; 4 Holkham; 5 Ixworth; 6 Raynham.

non-arable area: the area of linear features, woodland and grassland (Figure2.7, R^2=0.82, ANOVA DF=1,4, F=17.86 p<0.05). Clearly, the pattern of productivity is strongly influenced by the balance of arable to non-arable area: the greater the arable area the greater is the importance of productivity in January and February.

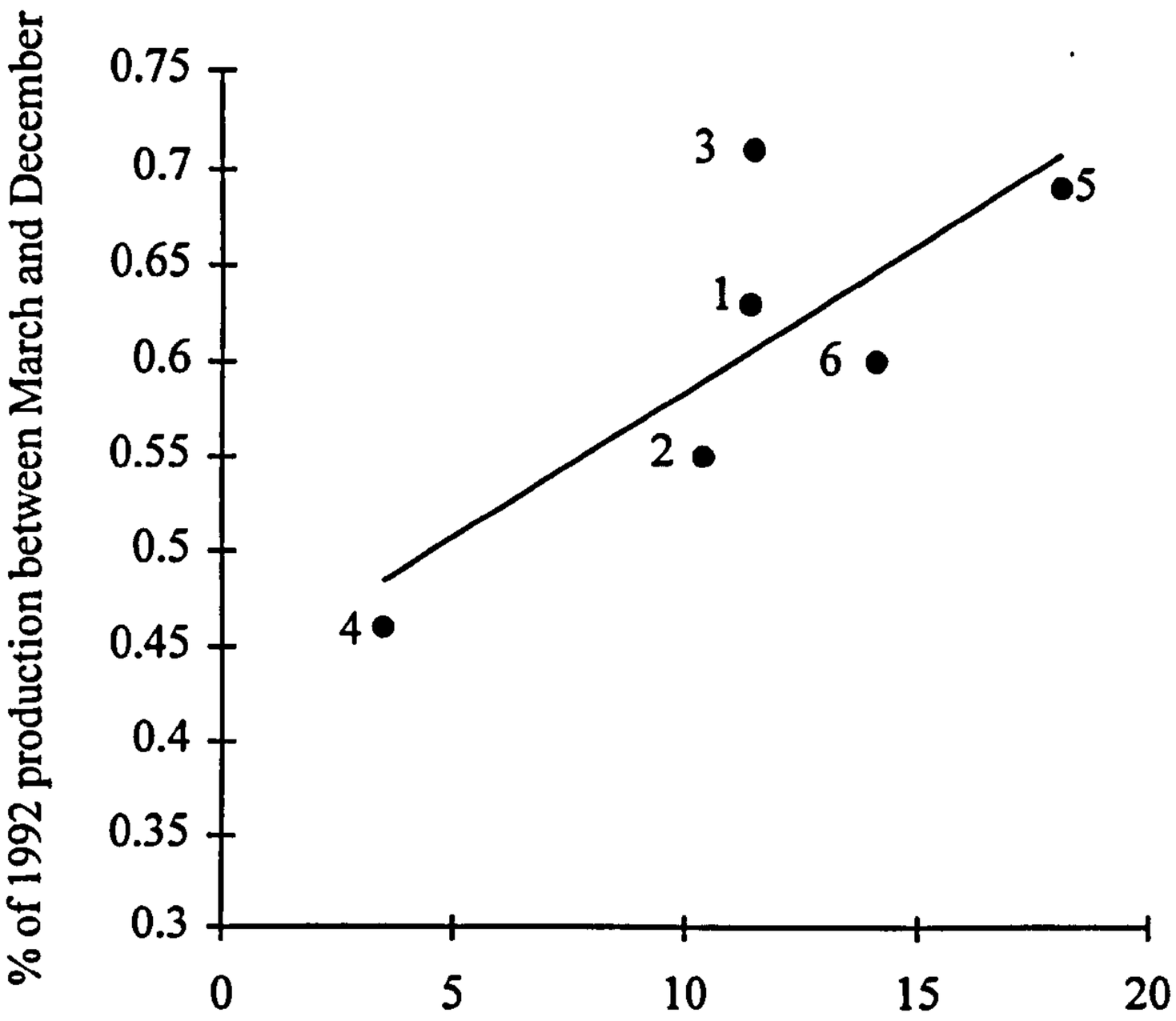
Surprisingly, those estates with the greater arable area, and therefore with the highest proportions of their total leveret production in January and February, have the greater density of hares.

The estimated pattern of survivorship of leverets born in 1992 to the February 1993 shoot is shown in Figure 2.8. A U shaped survivorship curve was found, with low survivorship in the period between March and July. The percentage of juveniles in the six study populations was not related to the recorded density (R^2=0.04, ANOVA DF=1,4, F=0.2, N.S.). The mean value of leveret survivorship in 1992 was 0.10, whilst a typical value of mean leveret survivorship is about 0.18 (Marboutin & Peroux 1995). For a population that means that recruitment of leverets into the next year would be reduced by 45%.

2.3.4 Diet analysis

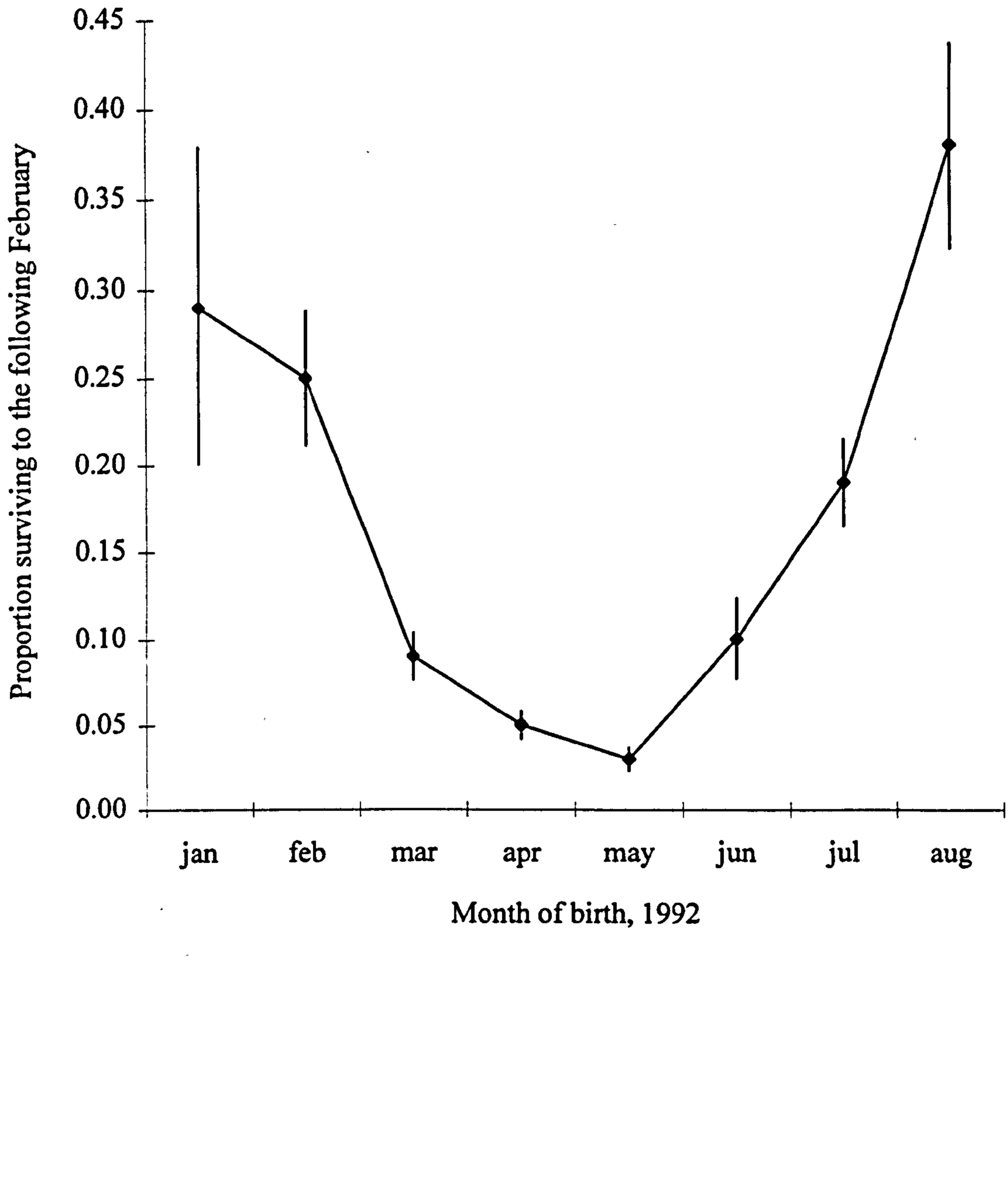
The diet consisted almost entirely of grasses which proved difficult to identify to the species level. The diet was therefore divided into winter cereals, other grasses, forbs, conifer and unidentified. The percentage of winter cereals in the diet is a minimum estimate, since some will probably have been identified as other grasses. Given the difficulties of identifying the grass species, and their overall abundance in the diet, the results were pooled between males and females to give an overall view of the diet composition. The February diet was therefore as follows: winter cereals 44%; other

Figure 2.7 The relationship between the proportion of births that occurred from March onwards on each site in 1992, and the area of linear features, woodland, grassland and scrub. The line is the regression equation, given as: summer production=0.92×% area+0.29.



The sites are numbered in the graph above as follows: 1 Euston; 2 Gayton; 3 Gazeley; 4 Holkham; 5 Ixworth; 6 Raynham.

Figure 2.8 The estimated survivorship of leverets (shown with standard error) born in 1992, to the February 1993 cull.



grasses 42%; forbs 7%, conifer 2%, unknown 5%.

2.3.5 1970s and 1993 population data compared

The age structures of the 1993 populations are summarised in Table 2.8. There was significant variation between the age structures of the cull data from 1972, 1974 and 1975 samples (χ^2 =15.09, DF=2, p<0.05) and also within the 1993 sample (χ^2 =44.36, DF=20, p<0.01). However, none of the individual samples had an age structure that was atypical when compared to the range of values found in the literature (e.g. see Broekhuizen 1979). When the leveret survivorship analysis was carried out using the age structure data from the 1970s samples, a similar pattern of survivorship was found (Figure2.9). Therefore, the critical low period of low leveret survivorship was also a feature of hare populations in the early 1970s. This is important because the fecundity data used to calculate the survivorship figures for the 1970s samples was estimated directly from hares shot during 1971 & 1972 (Lincoln 1974), meaning that these are likely to be very accurate estimates of survivorship.

2.3.6 Habitat change 1961-1992

The changes in abundance of the major crop types is given in Table 2.9. The information available on the amount of winter and spring cereals is also given. The major changes have been the expansion of winter planted wheat and oilseed rape. This has resulted in a reduced diversity of grass species in the arable landscape (Fig. 2.10). There has also been a trend to plant barley in winter instead of spring; in 1992 less than 50% of barley was spring planted (Britton 1990). This has meant that food in the form of cereals is abundant early in the year, but now increasingly scarce later

Table 2.9 Major crop changes in East Anglia, 1961-1992

Habitat	% change 1961-1992	Used as forage between *
wheat	+219	January - March
barley	-49	Depends on type
total winter cereals	+287	January - March
total spring cereals	-205	April - June
oilseed rape	+4566	Unknown
sugar beet	+52	Unknown
ley grass	-72	All year
permanent grass	-52	All year
rough grazing	-32	All year

* based on Tapper & Barnes (1986).

Figure 2.9 The survivorship of animals born in the 1970s. The data are based on culls from 1972 (Δ), 1974 (□) and 1975 (o).

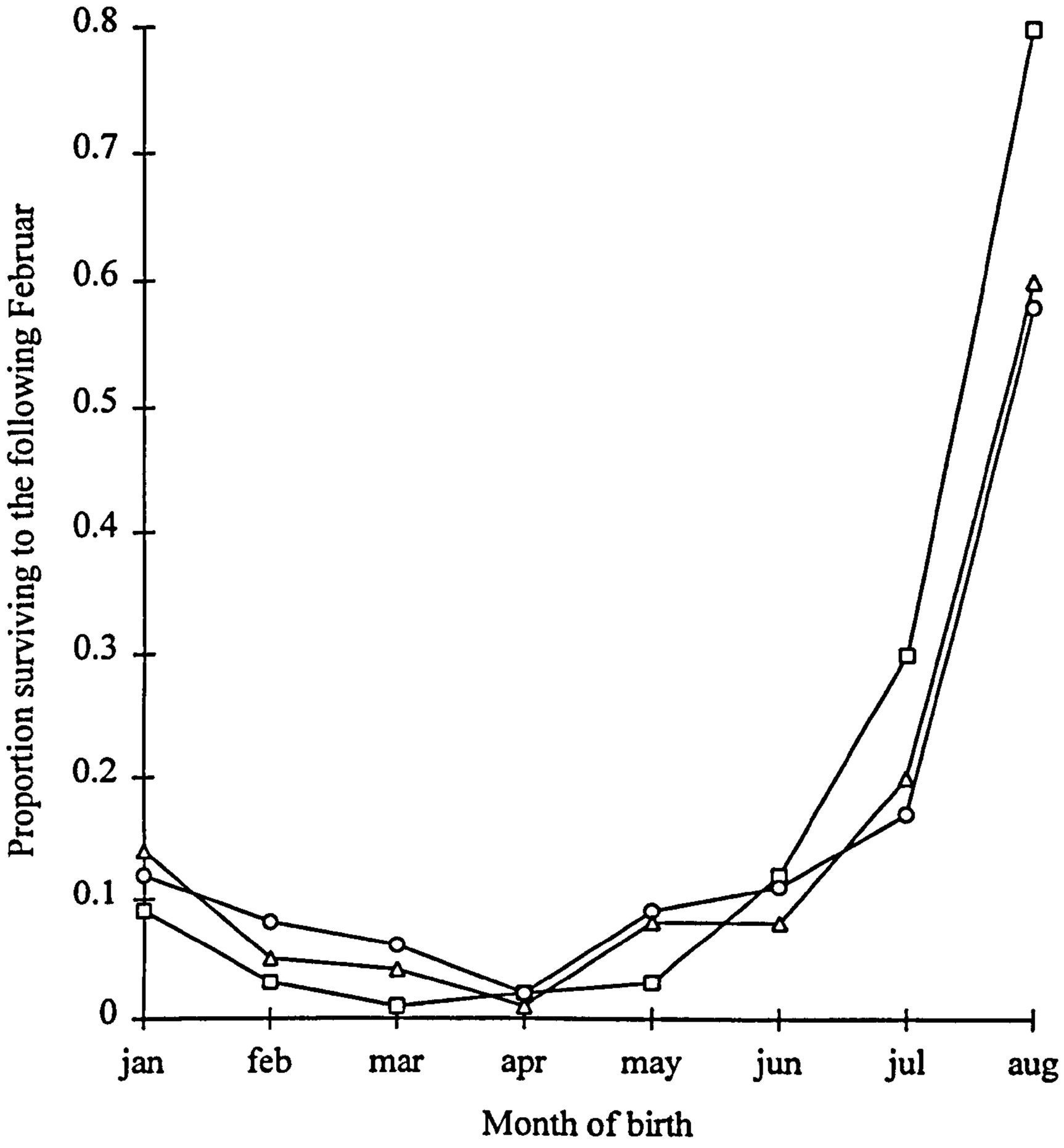
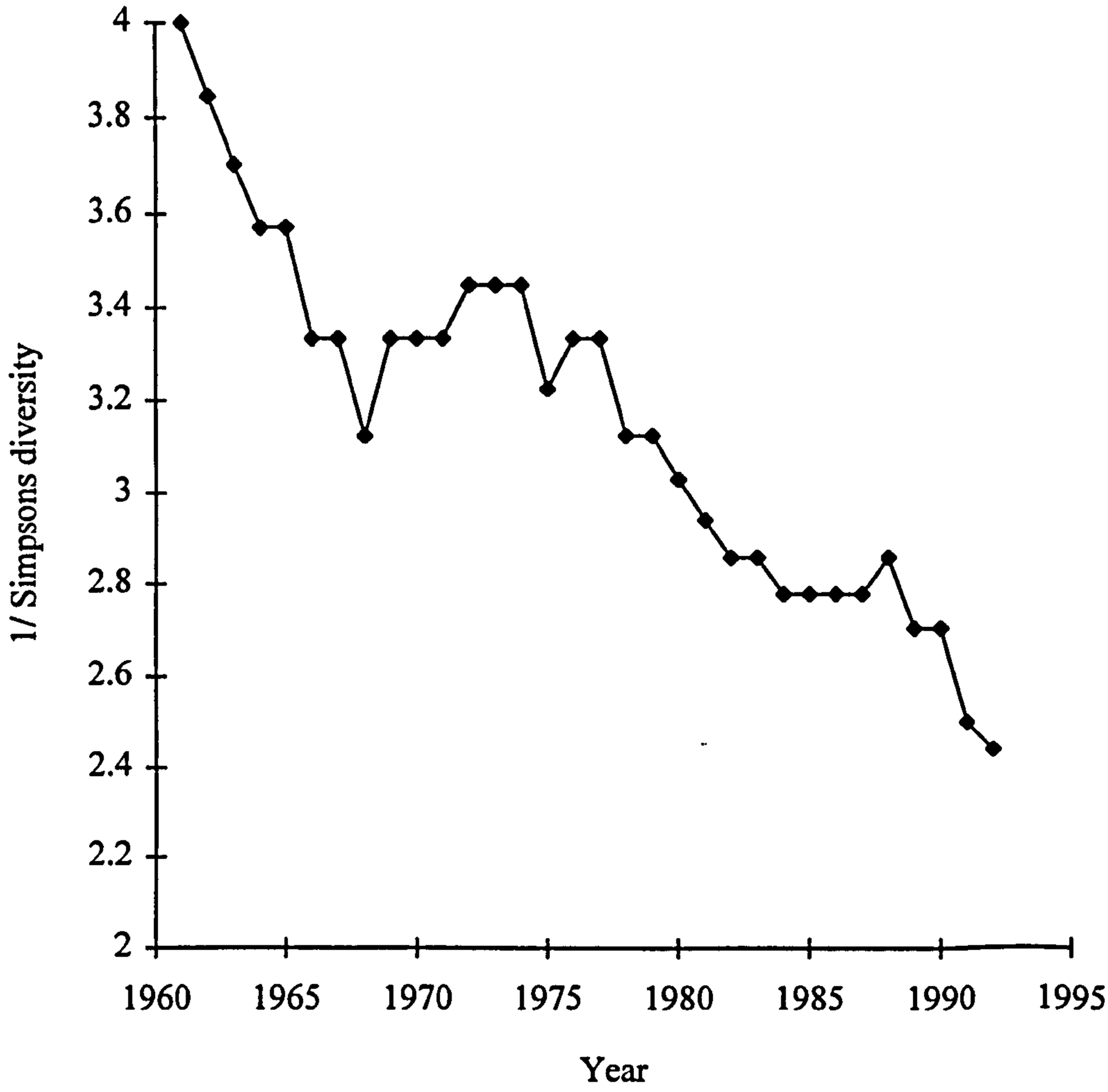


Figure 2.10 The loss of diversity of grasses in the arable landscape of East Anglia since 1961. Note that the diversity of grasses declined sharply during the early 1960s, when the hare population also suffered a large decline (see Figure 1.1, page 11).



in the year. Also much of the alternative grass forage (permanent, ley and rough grazings) has been lost.

2.4. Discussion

2.4.1 The status of the hare populations in February 1993

The densities of hares on the six study areas varied considerably, from 18 to over 60 hares per 100 ha, although none of the study areas reported that densities were atypical when compared to recent years. This is consistent with the 1992/3 hare survey of Great Britain, which found that hare numbers varied considerably, even in areas of similar habitat (Hutchings & Harris 1996). However, the densities in the six study areas are high relative to the rest of the country which, even in arable areas, typically has less than five hares per 100ha (Hutchings & Harris 1996).

Breeding had started in all the areas sampled, and at three sites lactating animals were found. Other studies have found a similar pattern of breeding at this time of year in Britain (Lloyd 1968; Lincoln 1974; Hewson & Taylor 1975), and at a comparable time at the beginning of the breeding season in New Zealand (Flux 1968). Births in January and February represented 16% of total recorded births in 1992, and therefore make a significant contribution to the population size. Comparing the data from the 1960s, 1970s and the 1990s, there was very little difference in the number of females breeding or the mean litter size; thus productivity early in the year was similar for both periods. Whilst the onset of breeding in hares is thought to be controlled by day-length (Caillol *et al.* 1992), the nutritional status of individual hares will play a role in determining when, after the appropriate

photoperiod stimulus, breeding will occur. Therefore there was no evidence that hares were suffering from poor nutrition or low reproductive output at the onset of the breeding season in 1993, compared to the 1970s or 1960s.

In addition, the greater the proportion of total births recorded from January and February 1992, the greater the population size 1993. This is likely to be the result of the high survivorship at the beginning of the year: the greater the survivorship then, the higher the population size.

2.4.2 The condition of the hares

Females were heavier than males as a result of continued weight gain after 200 days, the age at which males stopped growing. Associated with this, females >200 days old also had significantly greater full and empty stomach weights than males, although there were no significant differences between younger males and females. Since mean stomach weight was significantly heavier in lactating females, it would appear that a larger stomach is an adaptation to accommodate the greater food intake required for lactation.

The benefits for the increased weight gain by females is clear: heavier females have more offspring. However, females with no foetuses were found throughout almost the entire range of carcass weights, indicating that other factors, such as previous reproductive investment (Iason 1990), are involved in determining whether or not a female breeds. The importance of body weight to reproduction has been observed before (Broekhuizen & Maaskamp 1981), and it is also thought that survivorship is positively related to body weight (Marboutin *et al.* 1990). In February, kidney fat index reserves were related to the animal's sex and breeding

status: females had higher levels of kidney fat than males, which was then used up during lactation. Clearly, females deposit kidney fat in preparation for the demands of lactation, whilst in males there will be less demands for fat storage, so it is possible that they are leaner to reduce the costs of locomotion, or make escape behaviour more efficient. Under periods of limitation, condition is normally dependent on status, if there is a dominance hierarchy (Sinclair 1986), However, non-breeding and breeding females had equal levels of fat, indicating that food resources are unlikely to be an important factor in determining whether or not a female breeds at this time. It is clear, therefore, that in February, there is no hard evidence to suggest that hare populations are in any way stressed, or that they are not as productive as in earlier years. It is therefore unlikely that stresses early in the year (January and February) limit hare populations. However, from post-mortem samples, it is not clear why some adult females do not breed at this time, despite having apparently adequate levels of fat and stomach contents.

2.4.3 The effects of the farming landscape on brown hares

Density, potential leveret production, female carcass weight and male testis weight were all positively related to the relative area of winter cereals, plough, stubble and set-aside. The relationship in Figure 2.2 suggests that areas with increasing the proportion of farmland covered in these features by 25% could lead to a doubling of hare densities. This is in part because hares will be attracted to areas which have high quality food in abundance, and this mobility may explain why relatively small changes in the landscape can have such a drastic effect on hare numbers. Oilseed rape did not appear in the diet in February, and this is consistent with the

observations of Frylestam (1986), who found that hares avoided oilseed rape after December. This explains why it had a negative effect on hare populations in February, and also explains why the National brown hare survey found that oilseed rape was associated with high hare numbers between October and December (Hutchings & Harris 1996). The avoidance of oilseed rape by hares coincides with the development of glucosinulates in the plant (Frylestam 1986), and these compounds are known to have a deleterious effect on many vertebrate herbivores (Tapper 1989).

Winter cereals were the main component of the diet, and the remainder of the diet was largely other grasses, which may have been present in fields of stubble or plough, or in surrounding woods and hedges. This is consistent with other studies (Frylestam 1986; Tapper & Barnes 1986; Wray 1992) and this stresses the importance of winter cereals to hare populations at this time. In this study, hares from Holkham Euston and Raynham had higher quantities of food in their stomachs than animals from other sites. However, the stomach contents weight was not related to the arable area, or density. The relationships between density and the proportion of land under cultivation may therefore be a consequence of more than simple food availability. A possible factor is the dominance system of hares. Where the area of land under cultivation is less, or where there is more oilseed rape, there may be increased social pressure on the remaining arable areas, and as a result, reduced population size as animals disperse into other areas.

2.4.4 The pattern of productivity in 1992/3 and in the 1970s

The productivity in January and February played a very important role in maintaining population size in the 1993 sample. Animals born at this time, had a relatively high chance of surviving to the following February. However, in both the 1993 and 1970s samples, there was a period of very low leveret survivorship between March and July. The difference between the January - February and March - July periods was more marked in the 1993 sample than the 1970s samples, with the 1993 sample having greater leveret survivorship in January and February. Increased leveret survivorship in January and February is difficult to explain: it may be the result of decreased competition, since fewer leverets now survive in summer, alternatively it may have been the result of less severe winter weather. Whatever the reason, it is clear that leveret production in January and February is important, and acts to buffer populations which have low leveret survivorship in summer.

The values of leveret survivorship were based on the assumption that there has been no change in fecundity since the 1970s. For February 1993, this was certainly the case, with fecundity close to expected (section 2.4.1). Also, the overall number of births was not lower than expected in the 1970s (Table 2.1), and therefore 1970s survivorship data are likely to be accurate, although this study cannot determine changes in summer fecundity which may have occurred since 1970. However, in terms of both energy and nutrients, lactation and growth are more costly than gestation (McDonald *et al.* 1988), and therefore would be more sensitive to changes in the quality or quantity of food resources. These results suggest that hare

populations are limited by low leveret survivorship between March and July, such that recruitment may be reduced to 45% of expected levels..

2.4.5 The changing arable ecosystem 1961-1992

The most striking habitat change between 1961 and 1992 is the expansion of wheat, oilseed rape and sugar beet. This has meant that alternative crops and grasses have been lost. Tapper & Barnes (1986) concluded that hares require two main habitat features on arable land: young cereal crops for feeding and woodlands or hedgerows for shelter. Crops such as winter cereals (barley and wheat) are present for up to ten months before harvesting, but only provide suitable food for hares from January to March (Tapper & Barnes 1986). During this period they provide a valuable food source and can form a large component of the diet. The quality of young winter cereals as a food source is the likely reason that the survivorship of leverets born at the start of the year was high both in 1970s and 1992.

However, after March hares must find alternative food sources. The diversity of cereal and other grass types has declined markedly since 1961, with the decline of spring sown cereals and ley grass. Spring cereals are selected by hares as forage between April and July (Tapper & Barnes 1986), and arable areas with a mixture of spring and winter cereals, with areas of stubble and grass, could provide a year-round food supply for hares, with spring cereals contributing a large proportion of the summer diet (Tapper & Barnes 1986). In addition, the use of fertilisers and pesticides has increased markedly since the 1950s and 1960s (O'Connor & Shrubb 1986), and this is also likely to have influenced the food availability for hares. Fertilised crops free of pests grow faster, and more evenly, allowing less feeding time

for hares (before the crops get too tall for hares to eat) and also eliminate any patches of poor crops that might have provided feed after the main crop had grown tall. Therefore, in summer, in the much less diverse 1990s arable system, food is likely to be more scarce, with hares foraging in the increasingly patchy areas of woodland and hedgerow. As a consequence, on the six estates the relative productivity from March to the end of the year was related with the relative area of linear features, woodland and grass, all potential alternative sources of food, although these are not of the same quality as a young fertilised cereal crop. For an animal with a high basal metabolic rate (McNab 1986), the loss of quality forage is critical, particularly for lactating females, which have a significantly increased food intake. Therefore, the hypothesis formed here is that the quality and quantity of summer food limits the energy and nutrient exchange in hares, and acts to reduce the production and survivorship of leverets. This results in population limitation.

2.4.6 Conclusions - modern agriculture and brown hares

Clearly the effects of agricultural intensification on brown hare populations are complex. Even in the 1990s, hares can reach high densities on agricultural systems which have all the classic features of intensification; large field sizes, loss of field boundaries and woodlands, extensive areas of monoculture and the widespread use of chemicals. For the first two months of the year there was no evidence that agricultural intensification was having any detrimental effect on hares. However, hares have declined in these landscapes, and the most likely hypothesis to explain this is that low productivity in the summer has reduced population size, and is now the most important factor limiting hare populations. The likely cause of the summer

stress is the shortage of high quality food, caused by the loss of diversity in the arable ecosystem, which no longer provides a year round supply of high quality cereals and other grasses. It is now important to examine the consequences of low leveret survivorship for hare populations. In particular, it is important to determine if the observations made in this chapter could have been responsible for the decline of hare populations and to examine the consequences of low leveret survivorship for present and future hare populations.

2.5 Summary

(1) Samples of hares, obtained from culls held at six different sites in East Anglia during February 1992, were post-mortemed. Densities on all six sites were high compared to the rest of Great Britain, with one site having over 60 hares per km^2. However, hare densities in the East Anglia region have declined by over 75% since 1961, according to game bag figures.

(2) Breeding had started in all areas, and at three sites lactating females were found. The condition of the animals was good, and the diet was composed mostly of winter cereals, which were widely abundant at the time of the cull.

(3) Female body weight, density, male testis weight and leveret production were positively related with the proportion of winter cereals, plough, set-aside and stubble that covered the study area. The only other crop available to hares during February was oilseed rape. However, this was not found in the diet of hares.

(4) An analysis of the age structures of the population indicated that very few animals born in the period March to June 1992 survived to February 1993; in fact, animals born January and February 1992 had a much higher chance of surviving to the following February 1993 cull.

(5) Data on hare population age structures from culls held between 1970 - 1975 were also found to have the same pattern of survivorship as the 1990s sample. By 1970 however, the majority of the hare decline had occurred. Poor leveret survivorship between March and June was therefore identified as a possible factor limiting hare populations.

(6) Major changes in habitat between have occurred in East Anglia between 1961 and 1992, leading to a much reduced diversity of cereals and other grasses in the area. Winter cereals are now the dominant crop (covering up to 70% of some areas), but only provide food for hares during the winter months. Much of the summer forage has been lost, including spring cereals and ley grass.

(7) It is now crucial to test the hypothesis that low leveret survivorship caused the decline of hare populations. This requires two main tests: (i) can the low survivorship found in this study be shown to bring about the decline of hare populations; (ii) can data be found which directly show poor summer leveret survivorship, and can this be linked to food availability.

(8) In the next chapter, hare population dynamics data are modelled, to critically test the hypothesis that low leveret survivorship caused the decline of hare populations.

CHAPTER THREE

MODELLING HARE POPULATION DYNAMICS

3.1 Introduction

In chapter two, I showed that poor recruitment, brought about by a reduction in leveret survivorship is the most important factor limiting hare populations, and is therefore the most likely cause of their decline. The analysis in chapter two indicated that with the observed level of survivorship for animals born in 1992, recruitment in hare populations would be reduced by about 55%. If it is correct, this hypothesis must be consistent with two important observations. Firstly, a hare population which is subject to low leveret survivorship should decline in a similar pattern as has been observed in the real game bag data (see Figure 1.1). Secondly, the adult age structure of the declining population should remain unchanged, since in chapter two there was no evidence that the adult age structures of low density populations were different to high density ones.. However, it is not known if low survivorship alone is sufficient to have caused the decline of hare populations in East Anglia, or indeed, if a hare population exhibiting this pattern of leveret survivorship is viable. Experimental studies to examine these problems in the field would have to be large scale, long term projects. An alternative first step is to use mathematical models to understand the dynamics of hare populations, and examine the consequences of reduced leveret survivorship on model populations instead.

Mathematical models have been widely used in ecology. However, it is important to understand what a mathematical model represents, in terms of the ecological system under study. Patten (1971) described mathematical models as

representing a particular view of an ecological system, rather than being a real system in miniature. He further argues that a model is therefore a balance between realism and abstraction. Clearly, it is important to realise the scope and limitations of a model at the outset, and to understand fully which parts of the model represent real data, and which represent assumptions made about the system under study. With these caveats in mind, models can become a powerful tool for understanding how an ecological system works.

Models of population dynamics are most often used to examine the sensitivity of populations to changes in parameters such as mortality, and are also used to determine methods for the control or conservation of a species. For example, Smith & Trout (1994) used Leslie Matrix models to examine population growth in rabbits (*Oryctolagus cuniculus*), and examined the sensitivity of the population to changes in fecundity and mortality. The rabbit model proved to be very robust although, in this case, fecundity and mortality values were changed only by 10%. The model was then used to test the impact of different rabbit control strategies, involving the removal of adults or juveniles at different times of the year. This showed that the success of control strategies depended on two factors: the time of the control and the age of individuals trapped. If the trapping scheme was biased towards juveniles, the control strategy was best operated in mid-June; if adult biased, the control was most successful if operated at the end of December (Smith & Trout 1994). As this example clearly demonstrates, models allow for a wide array of tests to be carried out, and allow for sensitivity analysis, an approach which examines the impact of changes in the model parameters. Sensitivity analysis therefore distinguishes the importance of different parameters, and can be used to determine how realistic the model is.

The advantage of the Leslie matrix model is that it combines a lot of information on basic population parameters (mortality, fecundity and age structure) and uses them to calculate both the growth rate and the change in age structure of the population. This approach was developed by P.H. Leslie in 1948 and has proved to be an extremely useful in studies of population biology (Usher 1972). It has been widely used and extended in many different ways, for example, to include density dependence and stochasticity (Usher 1972). Stochasticity (random variation) is important since it is a feature of natural populations, and gives an indication of the ability of a population to withstand fluctuations in the environment. Under normal circumstances, variation in survivorship or fecundity, such as that caused by bad weather, is unlikely to cause a population to go extinct. However as the population declines toward zero, the chance of these events causing extinction increases. As a result, lower density populations are more unstable. Modelling has obvious applications for conservation biologists, who use 'population vulnerability analysis', to assesses the extinction risk for a given population size (Gilpin & Soule 1986). Population modelling can also be applied to brown hares and a lot of data are available from studies of hare populations. However, long term data on hare population dynamics are not available and, at present, modelling is the only feasible option to gain insight into the effects of reduced recruitment in hare populations.

In this chapter I use computer modelling to simulate changes in leveret survivorship in brown hare populations, to determine the extent to which leveret survivorship must change in order to replicate declines seen over the last thirty years in East Anglia (Tapper & Parsons 1984). The model will also examine the consequences

of changes in fecundity and adult survivorship for hare populations, and examines the stability of remaining hare populations. The sensitivity of hare populations to changes in survivorship and fecundity will also be assessed. In addition, the effects of culling hare populations will be examined to determine the possible role of culling in the decline of hare numbers, and the general consequences of culling for a hare population.

3.2 Methods

3.2.1 Modelling age structured populations: the Leslie matrix

The Leslie matrix model uses data on age structure, fecundity and survivorship, such that both fecundity and survivorship can change with age (as is observed in most species). The matrix is best thought of as a method of displaying data which makes performing calculations easier. It is useful to understand some of the mathematics of matrices in order to understand fully what the Leslie matrix does.

For the model, the age structure of the population is written in vector format, as [x1, x2, x3,...xn] where x is the number in each age class, up to age class n (e.g. [100, 40, 10, 5]). The sum of the age classes gives the population size. The model also uses data on age specific fecundity and survival.

The data are in the form of an age structured matrix:

age

	1	2	3	.....	x
	f1	f2	f3	.....	fx
	p1				
		p2			
				p_{x-1}	0

fx represents the fecundity of the females in the age class x, and px represents the probability of females surviving from one age class to the next. Note that in this form, the model is for females only, and that the empty cells are equal to zero but left blank in the diagram above for clarity. Also worth noting is that the final age class must have a zero chance of survivorship. To run the Leslie model, the fecundity and survivorship figures in the matrix are simply multiplied by the vector containing the corresponding age structure. When vectors and matrices are multiplied, the result is another vector, i.e. another set of age structure data. In other words, the age structure is multiplied by the fecundity - survivorship matrix and this produces another age structure. This can be repeated for as many years as needed. Thus, this type of model gives data on both changes in population size and age structure.

A further use of the model is that it can be used to estimate the rate of increase of a population (Usher 1972). This requires the calculation of eigenvalues, a term frequently mentioned in papers using the Leslie matrix. The eigenvalue (λ) is the value

which, when subtracted from the fecundity - survivorship matrix, gives the value of zero. For this calculation, λ must first be multiplied by a matrix whose left to right diagonal values are 1, and all other values are zero (creating a matrix whose left to right diagonal =λ, and all other values =0). The calculation is set so that the λ matrix is the same dimensions as the fecundity - survivorship matrix. To solve λ, the two matrices are subtracted. This creates a new single matrix, each row of which can be treated as a separate linear equation which is then solved for λ (Bulmer 1994). When λ =1, the population is stable, when λ is > 1, the population is increasing, and when λ is < 1 the population is decreasing. The per capita rate of increase of the population can be shown to be equal to ln λ (Usher 1972).

3.2.2 Modelling populations using RAMAS

RAMAS (© Applied Biomathematics 1988; Ferson & Akcakaya 1988) is a computer program which carries out the matrix and eigenvalue calculations outlined above. The program also allows for immigration and emigration to be included in the model, and produces results based on the entire population, not just females. Harvesting can be included in the model by removing the culled individuals from the affected age classes; in the model this is included as emigration. Random variation can also be included in the model; in this way several repeats of the calculations can be made, with slightly different values of fecundity and survivorship. Density dependence can also be included, in the form of the logistic model:

$$R=N[1+r(1-N/K)]$$

where the annual recruitment to the first age class, R, is a density dependent function of N - the number of leverets produced each year. In the model, K represents the

maximum recruitment that is possible, and r is the per capita growth rate of the population. Both r and K change when fecundity changes. K is calculated as the fecundity × the number of females; r is calculated from the matrix (see above). K can be thought of as determining the level of abundance a population attains, and r the speed with which it reaches this level. As N approaches K, the annual recruitment R becomes equal to the number of leverets produced, and the population stabilises.

3.2.3 Creating a model hare population

Table 3.1 summarises the information used in the RAMAS model. The model calculates the total population size as the sum of the adult population (age greater than zero). The figures for fecundity and survivorship are based on the figures given in chapter 2. The eigenvalue of the survivorship fecundity matrix is used to determine the stability of the model population. For the initial population, the eigenvalue is expected to be close to one, indicating a stable population.

Stochasticity was introduced into the model by adding a coefficient of variation into the estimates of survivorship and fecundity. The variation added in this model gives about a twenty percent variation in both parameters. Using this variation, RAMAS calculates the probability of a temporary decline. This plots the probability of occurrence of a 0 to 100 percent decline of the population (probability-decline analysis). This is based on the high and low values which the population size reaches during 50 replications of the model, each slightly different as a result of stochasticity. The probability of the population declining to a particular level is then calculated from the number of times this level is reached during the simulations (Ferson & Akcakaya 1988). Generally, the probability is a decreasing function of the percentage decline, such that a

Table 3.1 The initial data used in the RAMAS model. The sources for the data are explained in the text.

Age class	Number in age class	Culled animals	Fecundity	Survivorship
0	1350	-	0	0.16
1	175	0.0	10	0.40
2	65	0.0	10	0.40
3	22	0.0	10	0.40
4	9	0.0	10	0.40
5	4	0.0	10	0.40

The initial adult population size was equal to 275. For the initial model no animals were culled, but in later models animals were removed from the population.

100% decline is much less probable than a 5% or 10 % decline. It is worth noting that because of the way this function is calculated, the probability of decline to a certain level can be zero. A comparison of these graphs provides an indication of the overall stability of the populations.

From this initial, stable population, a declining hare population is then simulated by decreasing leveret survivorship, adult survivorship or fecundity. In this model, leveret survivorship is modelled as an overall level. The average figure for leveret survivorship in 1992, using the data from chapter two, was 0.10 (see chapter two). Typical figures quoted for leveret survivorship are about 0.18, (Marboutin & Peroux 1995). Thus, it is predicted that the model population should be stable with leveret survivorship values at 0.18, and decline as leveret survivorship is lowered. In addition, reduced fecundity and adult survivorship were also modelled, in order to examine the consequences for a hare population.

3.2.4 The model scenarios

Five types of scenarios are presented: in the first four it is assumed that the change in parameter has been abrupt, i.e. in the model survivorship or fecundity is immediately reduced from normal levels In the four following scenarios : (1) leveret survivorship was reduced from 18% to 12%, 8%, 6% and 4%; (2) fecundity was reduced from 10 to 8, 6, 4 and 2; (3) adult survivorship is reduced, evenly across the age classes from 30% to 25%, 20%, 15% and 10%; (4) fecundity and leveret survivorship were reduced together such that when fecundity = 7, 5, 3, 1, leveret survivorship = 14%, 11%, 6% and 2% respectively. In the fifth case, the change in parameter was be applied gradually. In this case, the aim is to realistically assess the changes that occurred in the fecundity and

survivorship of hares over the period 1961-1992. This is important because habitat change has been gradual, yet the nature of the hare decline has not: it has been characterised by a sharp decline over the first five years followed by a much slower rate of decline, then reaching apparent stability in the last five to ten years. Clearly, it is important to understand in what way fecundity and survivorship must change in order to create this kind of decline pattern.

For each of these cases 50 repeats were carried out, each one slightly different as a result of the stochasticity applied to the fecundity and survivorship values. Each simulation lasted 30 years, thus representing the period 1961-1991, over which hare numbers declined in East Anglia by over 75% (Tapper & Parsons 1984).

3.2.5 Comparing the model data with real data

For this chapter, the predictions of population change generated by the models are compared with real game bag data (Tapper & Parsons1984). The game bag figures are given in chapter one (Figure 1.1) and have two important characteristics: a steep initial decline followed by a gradual reduction in numbers, eventually reaching apparent stability. Clearly, if the models presented in this chapter represent the real system, then the change in numbers predicted by these models should show a similar pattern. For most of the graphs, standard deviation figures are provided, rather than standard errors, since the aim is to show the degree to which the population is likely to decline, rather than express the accuracy of the mean.

3.2.6 Estimating the sensitivity of hare populations

The sensitivity of hare populations to changes in fecundity and survivorship is examined by plotting the change in λ with change in the parameter: the steeper the change in λ, the more sensitive the population growth rate is to changes in the parameter. This method has been used before (e.g. Marboutin & Peroux 1995) and has the advantage that it directly links population growth rate to the change in parameter, and this is often more easily interpreted than more abstract measures such as change in extinction probabilities (see section 3.2.3).

3.2.7 Modelling the annual cull

To simulate a cull in RAMAS, members of the adult population were removed from the model in each year of a thirty year simulation. It was assumed that the cull affects the age classes evenly, and thus the same percentage of animals were removed from each age class. The data in the model were the same as those used in the initial model used above (see section 3.2.3 and Table 3.1). As in the models above, density dependence and stochasticity are added to the model, and fifty repeats of each model were then run. Initially, 10% of the adults are removed from each age class, then in subsequent models the percentage killed was increased in multiples of 10%.

It is also worth noting that RAMAS assumes that animals in the population breed and then die. Therefore, in this simulation it is assumed that the animals breed, and some are then shot, and then the remaining animals breed. The pattern of breeding followed by culling is then repeated year after year on the remaining animals. However, annual hare shoots mostly occur at the start of the breeding season, whereas this simulation assumes the cull is at the end of the breeding season. The most important

consequence of this will be that the in the first year of the simulation, animals will not be shot before they breed, meaning that the effects of shooting will be delayed until the second year of the simulation.

3.3 Results

3.3.1 The model hare population

The initial hare population size was scaled to be between 250 and 300 animals at equilibrium density; this is equal to the number of hares found in a $10km^2$ area of East Anglia in 1960 (pre decline), as shown by game bag records (Tapper & Parsons 1984). The model population was found to be stable, with an overall mean value of λ close to one (1.16) for fifty replications of the model. The population was found to be closest to stability (λ=1.00) when leveret survivorship was reduced from 0.18 to 0.16. Below 0.16 the population started to decline (λ<1.00). Therefore, the age structure found in chapter two, with a typical value of leveret survivorship and a fecundity of 10 was found to be stable. However, the population fluctuated widely as a result of stochastic variation, and this was reduced with the introduction of density dependence (Figure 3.1), using values for r, the intrinsic rate of population increase as 0.8, and k, the maximum number of leverets that can be produced, as 1350. The introduction of density dependence did not change the tendency for the population to remain stable (λ=1.00), and acted only to reduce the wide fluctuations which occurred in the initial model.

For the rest of the analysis, it is assumed that density dependant factors operate. These act to reduce the fluctuations within the data, counteracting the stochastic effects, but do

not affect the trend of the populations to decline or increase as fecundity and survivorship change.

The probability-decline analysis indicated that for a stable hare population, with density dependence, there was a zero percent chance of a 75% percent decline: this means that the real hare decline was extremely unlikely to have occurred by chance (Figure 3.2).

3.3.2 The effects of reducing survivorship

When the initial hare population was subjected to reduced levels of leveret survivorship, the population declined (Figure 3.3). Declines, similar to that of the real populations of East Anglia occurred when leveret survivorship was reduced by half, from 0.16 to 0.08 (Figure 3.3) The population proved to be highly sensitive to changes in leveret survivorship with the growth rate of the population declining rapidly with changes in leveret survivorship that were greater than about 10% (Figure 3.4). Variation in leveret survivorship is thus clearly a very important factor in determining year to year variation in hare populations. The adult age structures of the populations with reduced leveret survivorship were not significantly different from the initial stable population (Table 3.2).

Populations that had a low leveret survivorship were also at much greater risk of going extinct than a pre-decline population (Figure 3.2). This analysis indicates, that for a population with leveret survivorship reduced by half, the probability of going extinct was 0.28, and the probability of a 90% reduction in numbers was almost 0.90: clearly this could play a major role in explaining why hare populations in East Anglia tend to be very variable (Hutchings & Harris 1996).

Figure 3.1 The population trend of the initial model population, with density dependence. The x-axis shows the years 1960 to 1990, to allow a comparison with the game bag data (chapter one, Figure 1.1). The error bars represent the standard deviation of the mean population size.

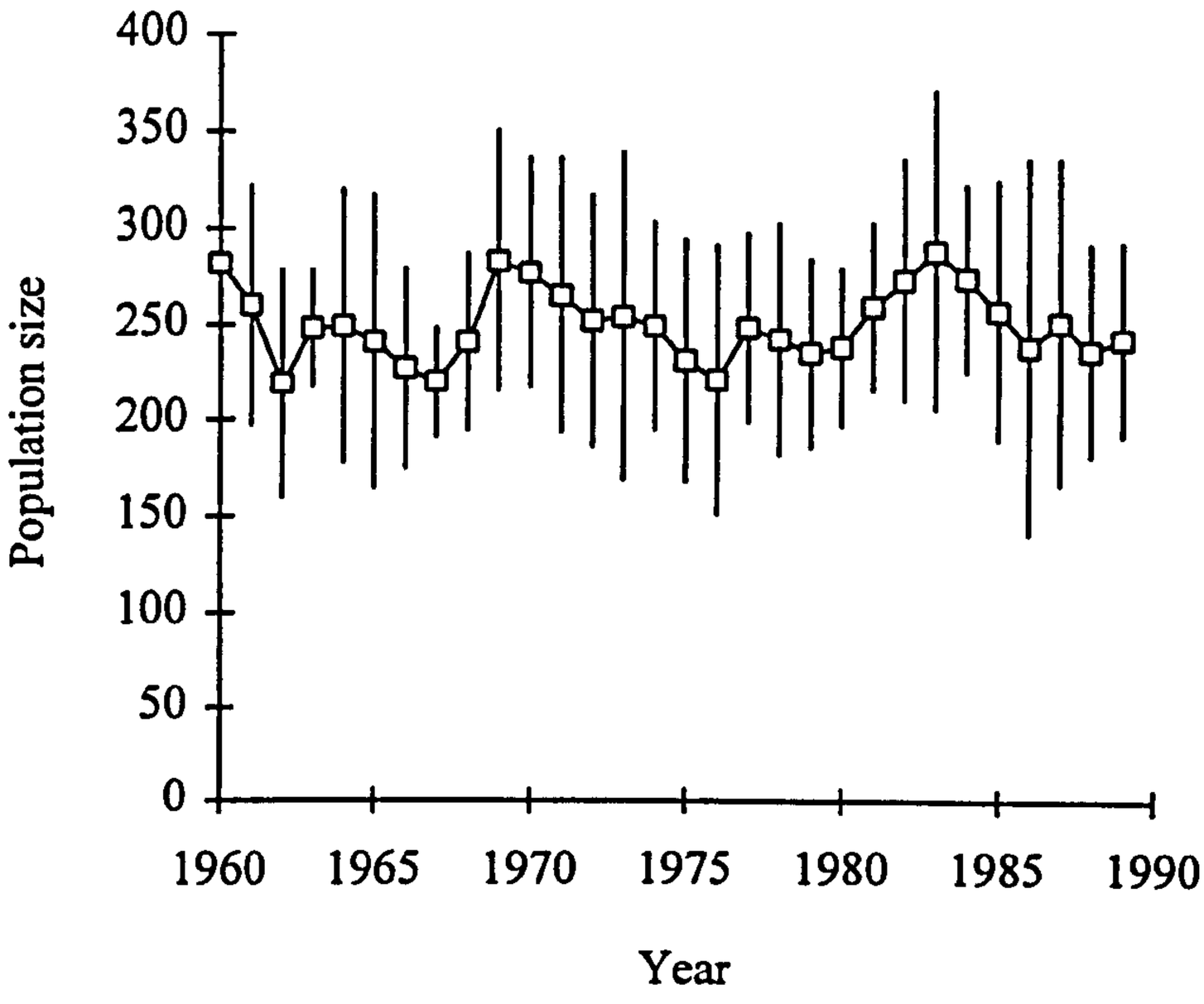


Figure 3.2 The probability of a percentage decline of the stable population shown in Figure 3.1, with density dependence (Δ), and a population at reduced density as a result of reducing leveret survivorship by half (•).

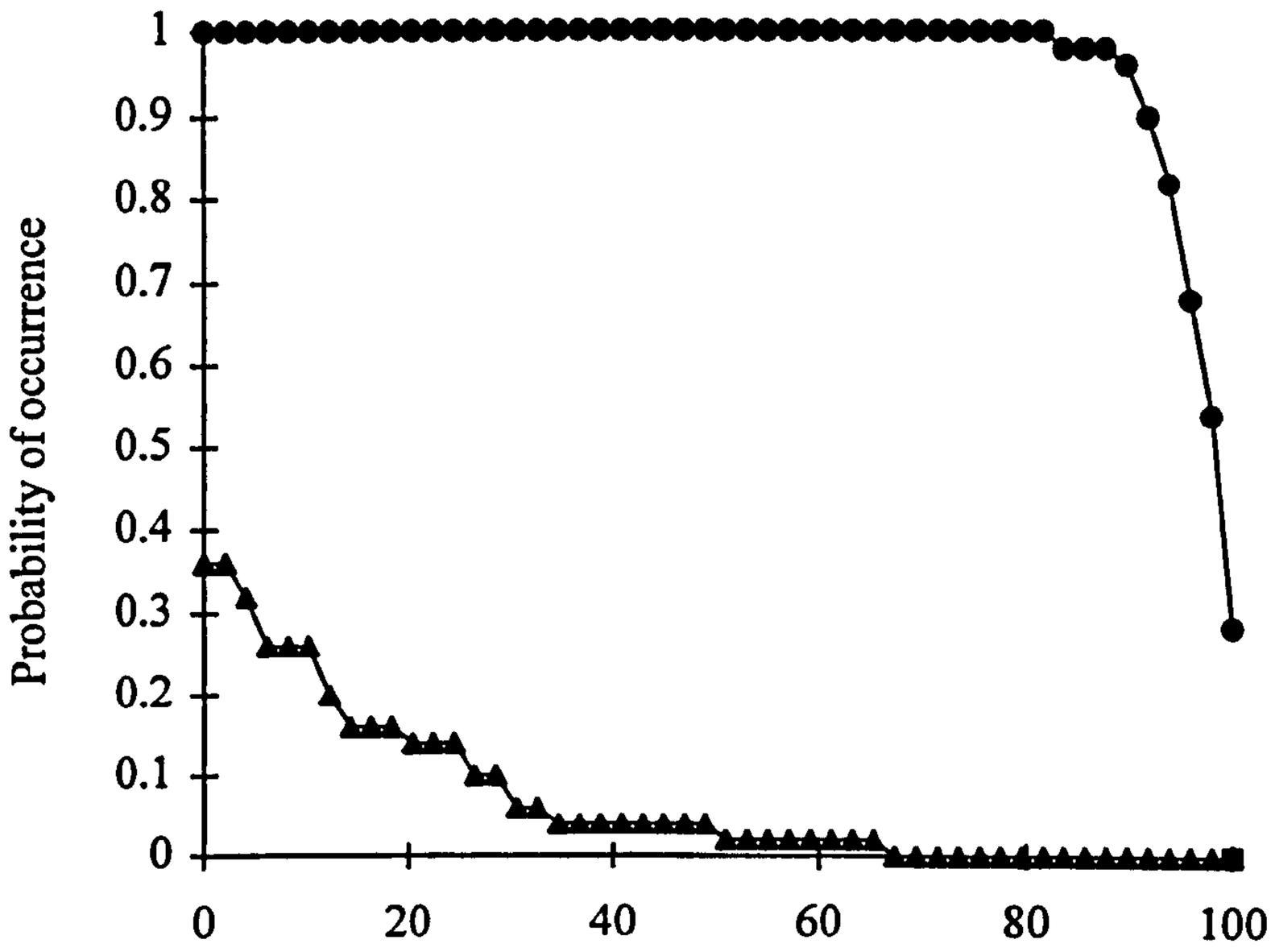


Figure 3.3 The effects of reducing leveret survivorship on a model hare population. Two scenarios are presented: in the first, survivorship has been reduced to 0.08 (•), and in the second it has been reduced to 0.06 (□). The x-axis has been scaled between 1960 and 1990 to allow for a comparison with the real game bag data (Δ). Error bars have not been shown for clarity, but the standard deviations of the model populations in this figure were of a similar magnitude to those in Figure 3.1.

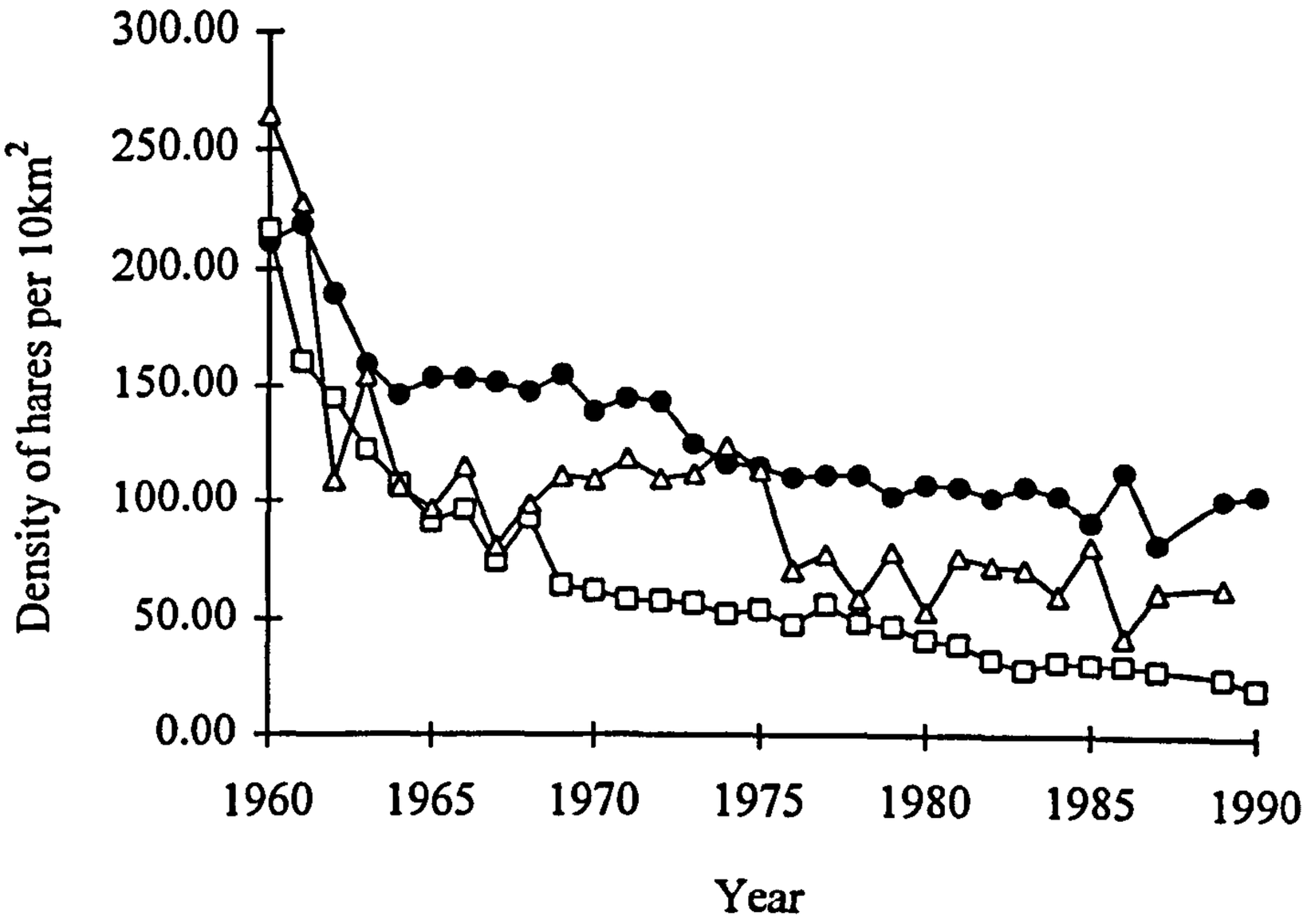
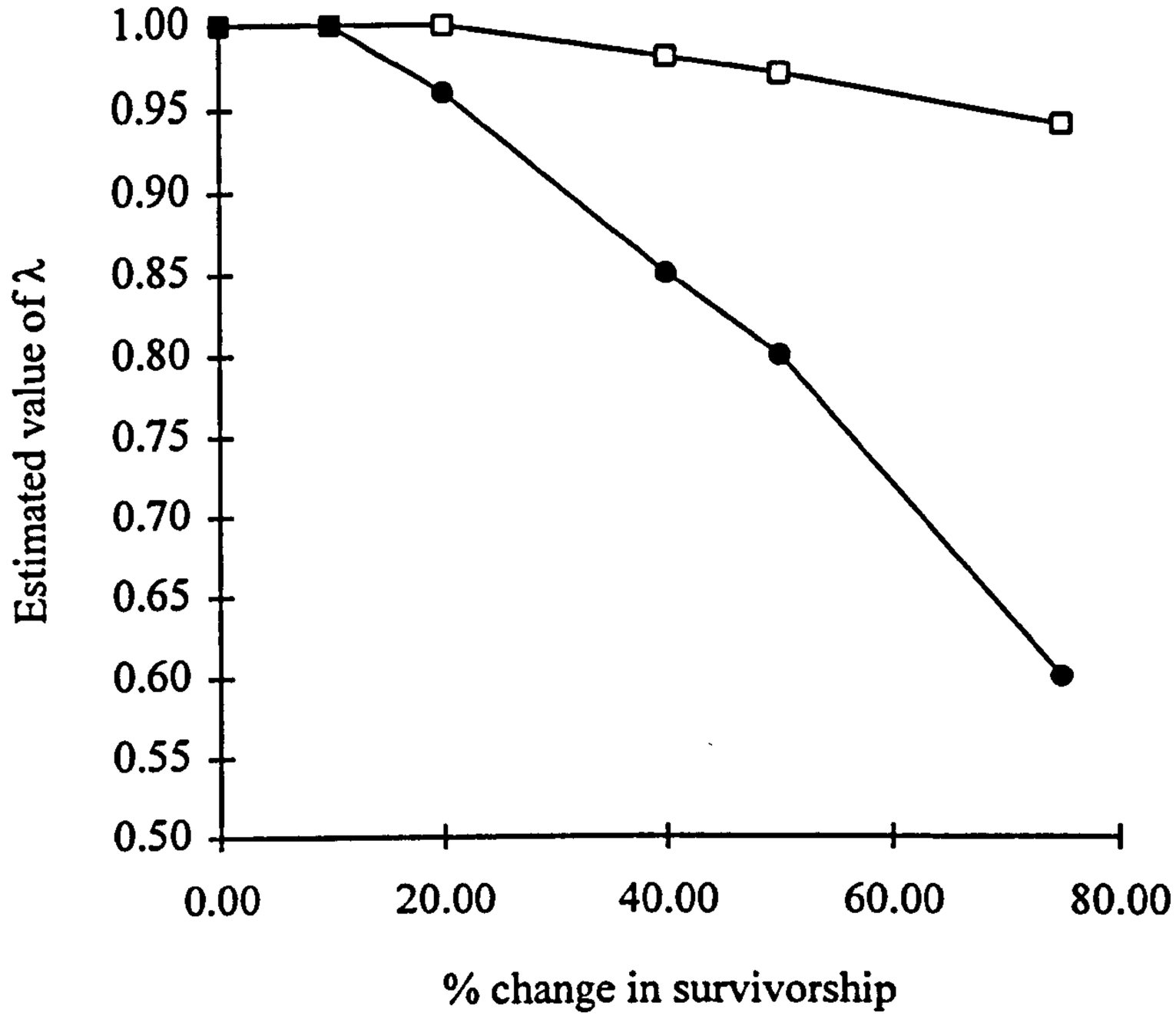


Figure 3.4 The sensitivity of hare populations to changes in survivorship of leverets (•) and adults (□), expressed as change in λ plotted against % change in survivorship.



However, when models of gradual change in leveret survivorship were applied, it was found that similarly gradual declines were observed: there were no initial steep declines as were observed in the real data. For example, a model whereby fecundity was reduced by one leveret every five years produced a decline which was gradual (Figure 3.5), and in fact, a drop in fecundity of 4 leverets was required in the first year to simulate the steep decline found in the game bag figures (Figure 3.3). This suggests that either the change in survivorship was sudden and large, or that additional factors are required to explain the initial steep declines in the real data.

3.3.3 The effects of reducing fecundity

The effect of reducing fecundity is shown in Figure 3.6. Each of the four scenarios presented create population declines, and the results indicate that to cause a decline of the same magnitude as has occurred in East Anglia, the fecundity of females would have to be reduced by half. Thus, as with survivorship, when recruitment into year class one is reduced by half, the model population declines in a manner similar to that of the real decline. The final age structures of the stable populations in Figure 3.6 are shown in Table 3.2. The adult age structures of the lower populations were not significantly different from the initial stable population (Table 3.2). Thus a hare population that exhibits low fecundity would not show any significant change in adult age structure.

As with survivorship, the population proved to be very sensitive to changes in fecundity, with λ changing markedly with reduced fecundity - in fact the sensitivity of the population to fecundity was nearly identical to that of leveret survivorship (Figure 3.4). Clearly, year to year variation in fecundity would have important consequences

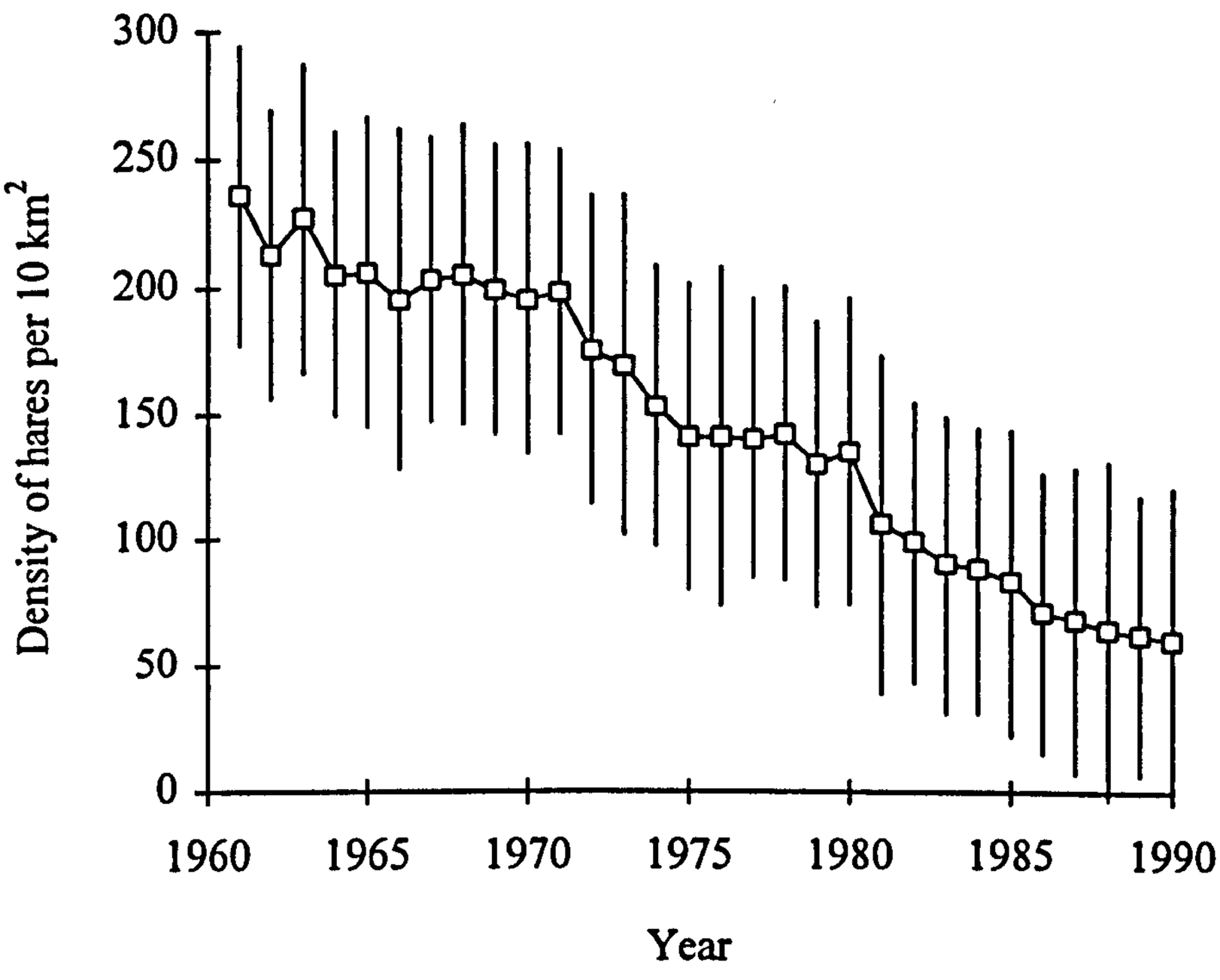
Table 3.2 The final adult age structures of the model populations. These data represent the mean age structure at the end of the thirty year simulations, for the different models of reduced survivorship and fecundity. In each case, the data represents the model which most closely matched the game bag data. These data are compared with the initial age structure of the model population.

Age class	Initial	leveret survivorship[1]	fecundity[2]	fecundity & leveret survivorship[3]	adult survivorship[4]
1	175	63	60	62	130
2	65	34	30	22	12
3	22	16	9	12	1
4	9	8	4	4	0
5	4	1	2	1	0

1. Leveret survivorship refers to the final age structure when leveret survivorship =0.07, see Figure 3.2;
2. Fecundity refers to the final age structure when fecundity =5, see Figure 3.3;
3. Fecundity and leveret survivorship refers to the final age structure when Fecundity=7 and leveret survivorship=0.08, see Figure 3.4;
4. Adult survivorship refers to the final age structure when adult survivorship=0.10, see Figure 3.5.

The age structure of Figure 3.5 is significantly different from the others, χ^2=69.0, DF=23, p<0.001.

Figure 3.5. The effect of gradual change in leveret survivorship on the density of a hare population. In this model, leveret survivorship was lowered to 0.12 in the first ten years, 0.10 in the second ten years and 0.08 in the last ten years (for comparison with other figure the x-axis is scaled between 1960 and 1990). When gradual models like these were applied, a gradual change in abundance occurred, and there was no crash in numbers in the early years of the simulation, as is observed in the game bag data (see Figure 3.3). The bars represent the standard deviation of the mean.



for a hare population. When a model of gradual change in fecundity was applied, as with leveret survivorship, gradual declines in the population occurred (Figure 3.7).

Clearly, reducing fecundity and leveret survivorship have the same effect for hare populations: both cut recruitment, which is a vital component of hare populations. This analysis indicates that a drop in recruitment of fifty percent is required to re-create declines in the model population which mimic the declines shown in the real data. It also shows that there are important consequences for the stability and future of hare populations that have undergone recent declines caused by low recruitment.

3.3.4 The effects of reducing survivorship and fecundity simultaneously

Reduced recruitment can, of course, be brought about by reducing fecundity and leveret survivorship simultaneously. As with the previous simulations, to produce a decline similar to that observed in East Anglia since 1961, the overall number of leverets reaching year class one must be reduced by half, an example of which is shown in Figure 3.8. Neither reduced leveret survivorship, or combined changes in fecundity and survivorship had any significant effect on the age structure of the population (Table 3.2). Clearly, if a combined reduction in fecundity and leveret survivorship had occurred, then apparently small changes in these parameters could bring about a very significant decline in hare numbers.

Similarly, populations that had reduced levels of fecundity and leveret survivorship were highly unstable (Figure 3.9), showing the typical high risks of going extinct that were not seen with pre-decline populations.

Figure 3.6 The effects of reducing fecundity on a model hare population. Two scenarios are presented here: in the first, fecundity has been reduced from eight to six (□) , in the second fecundity has been reduced to five (•). The x-axis has been scaled between 1960 and 1990 to allow for a comparison with the real game bag data (Δ). Error bars have not been shown for clarity, but the standard deviations of the model populations in this figure were of a similar magnitude to those in Figure 3.1.

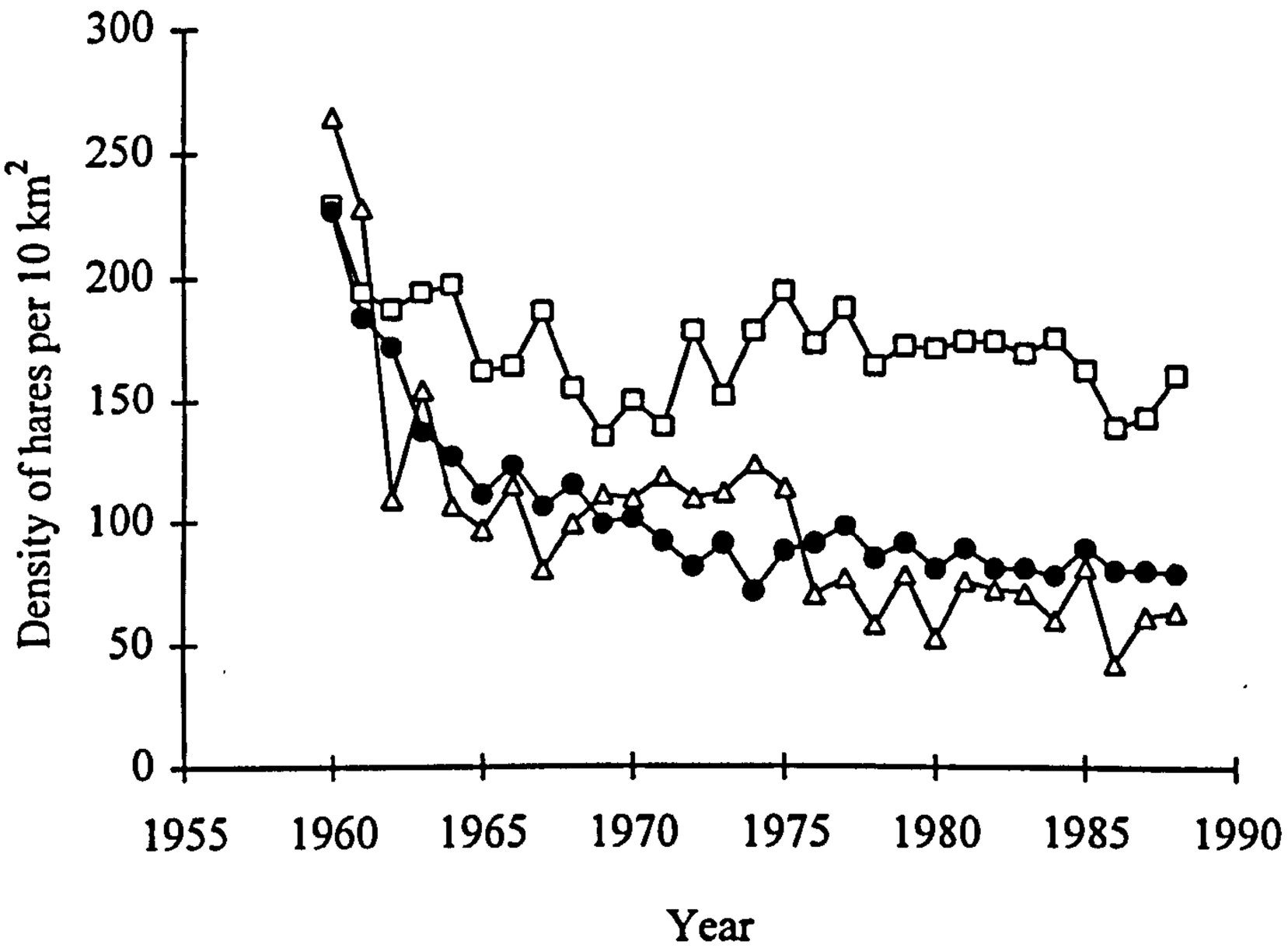
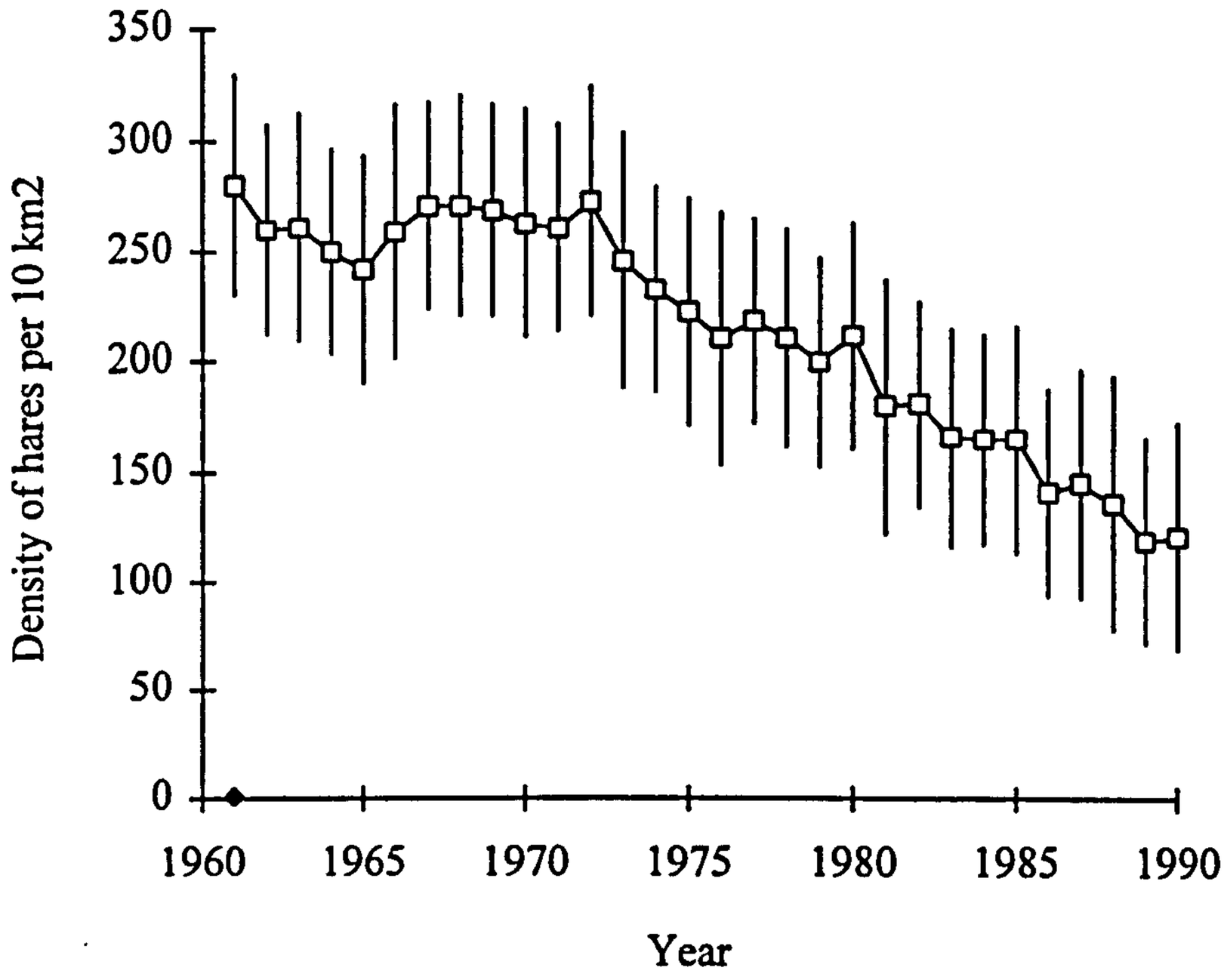


Figure 3.7 Gradual changes in fecundity brought about similar declines as did gradual changes in leveret survivorship (Figure 3.5), an example of which is shown here. In the first ten years of this simulation, fecundity is reduced to eight, in the second ten years it is reduced to six, and in the last ten years it is reduced to five. The bars represent the standard deviation of the mean.



3.3.5 The effect of changes in adult survivorship

The population proved also to be sensitive to changes in adult survivorship (Figure 3.10), although the change in population growth (λ) was less strongly influenced by change in adult survivorship than by fecundity or leveret survivorship. Adult survivorship had to be reduced from 0.4 to 0.1 to bring about a 75% decline in numbers (Figure 3.10). Even though the change in adult survivorship was spread evenly across the age classes, when adult survivorship was reduced, the effect on age structure was significant (Table 3.2). Changes in adult survivorship could bring about yearly variation in hare numbers, but this is likely to be less important than changes in fecundity and leveret survivorship. In addition, very marked changes in the age structure of a population would occur if adult survivorship was reduced.

3.3.7 The effects of shooting

Despite the population being less sensitive to changes in adult survivorship than fecundity or leveret survivorship, the population declined rapidly when an annual shoot killed more than 10% of the adult individuals. A sustainable shoot for a closed population was therefore obtained only when fewer than 10% of the adults were shot (Figure 3.11). Even the minimum estimate for the numbers of hares shot in a cull is higher than this, at 40% (Tapper & Stoate 1991). Culls could therefore have a very significant effect on a population if there were not any compensating factors, such as immigration which buffered the culled population. I t is a component of the Leslie matrix that makes a model population more susceptible to shooting than changes in adult survivorship. When adult survivorship is reduced, the adult animals are available to breed up to and including the last year of their life , whereas, when the animals

Figure 3.8 This figure shows a combined reduction in fecundity and leveret survivorship (fecundity = 7, leveret survivorship = 0.11) such that overall, recruitment would be reduced by half of the stable level (•). For a stable population, recruitment (per female, per year) is 10×0.16 = 1.6, in this example, the recruitment per female, per year is 7 × 0.11 = 0.77. As in the previous figures, comparable game bag data are provided (Δ). The bars represent one standard deviation.

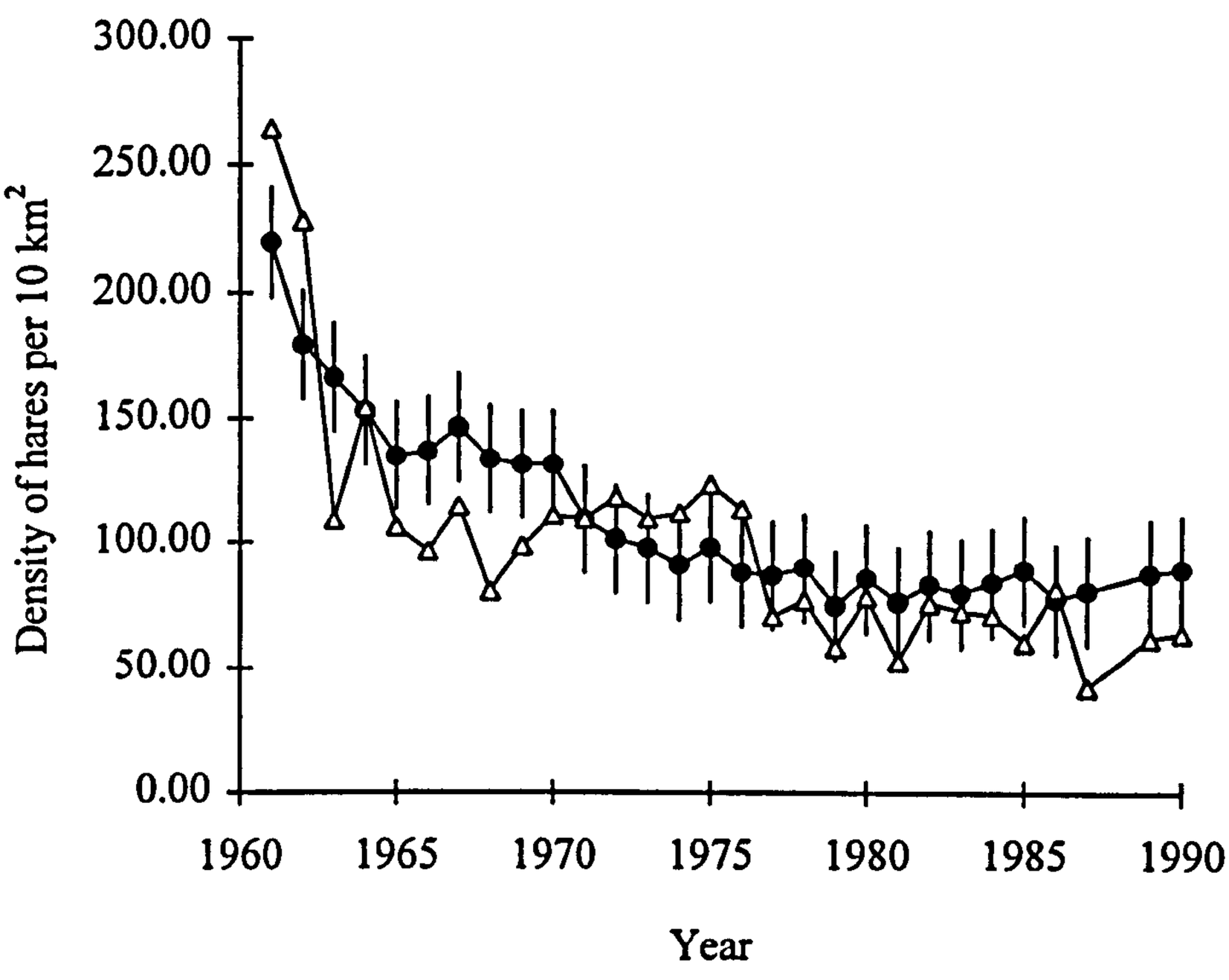


Figure 3.9 The probability of a percentage decline of a population that has been reduced by low fecundity and leveret survivorship (fecundity=7; leveret survivorship=0.11). This population is apparently more stable than one which has only fecundity or survivorship reduced (see Figure 3.2). The population is, however, still likely to undergo declines of up to 40%.

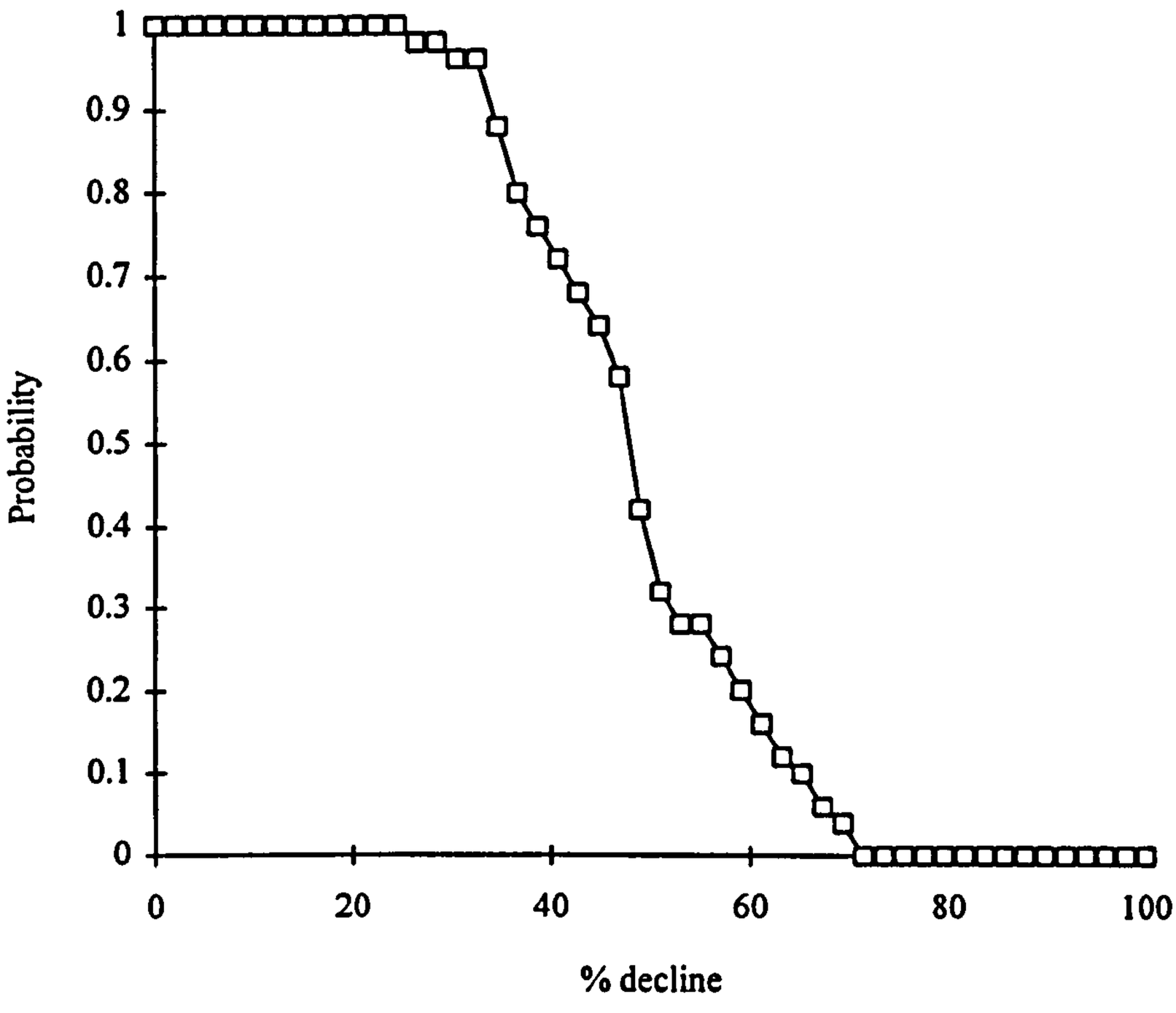


Figure 3.10. The effect of changes in adult survivorship on density. When adult survivorship is 0.3 (Δ) the population only declines slightly, but the declines become greater when adult survivorship is reduced further to 0.2 (□) and to 0.1 (•) when the decline is comparable to the game bag data (×). The standard errors in these data are comparable to those in the other figures, and have been left out for clarity.

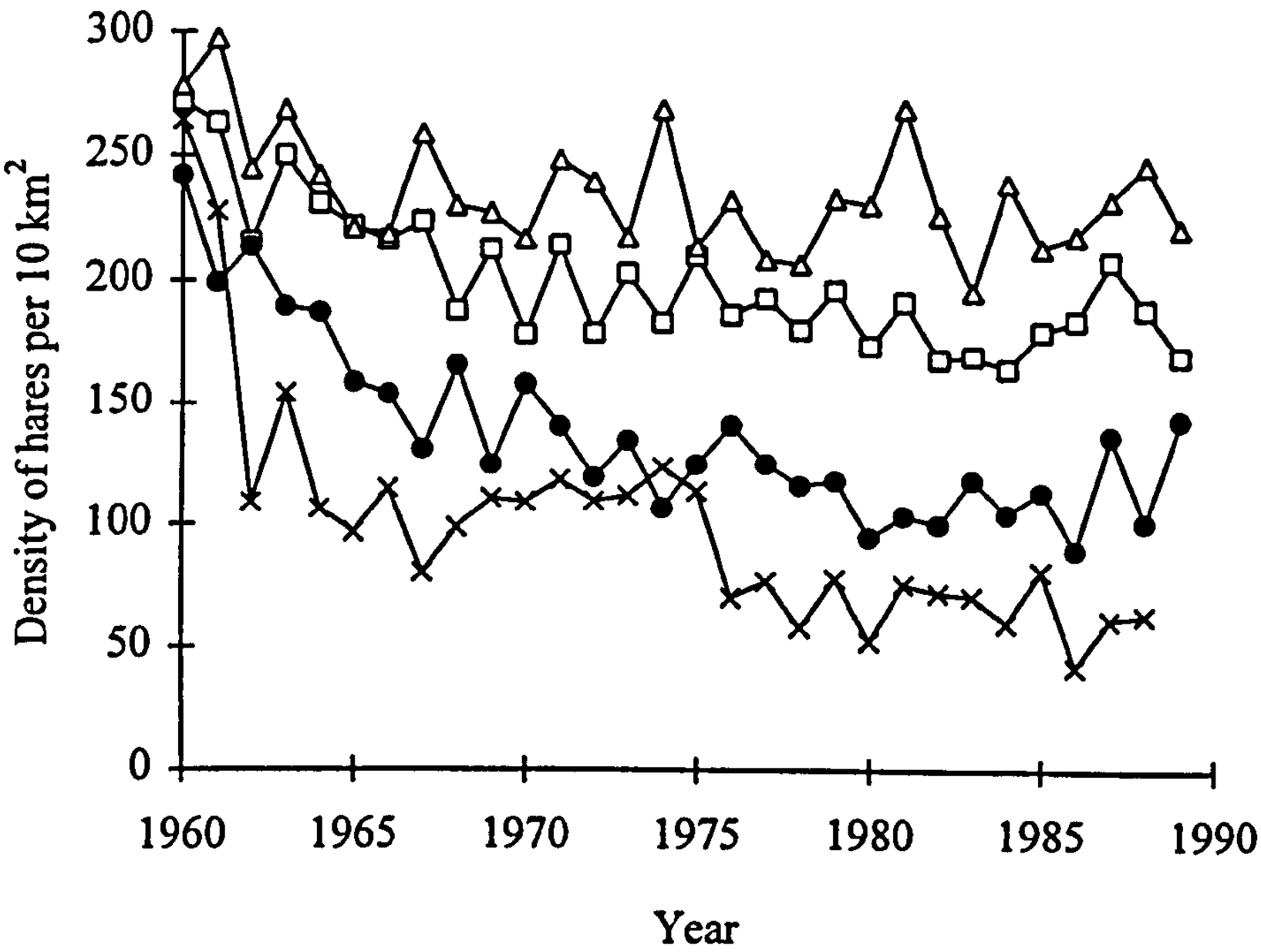
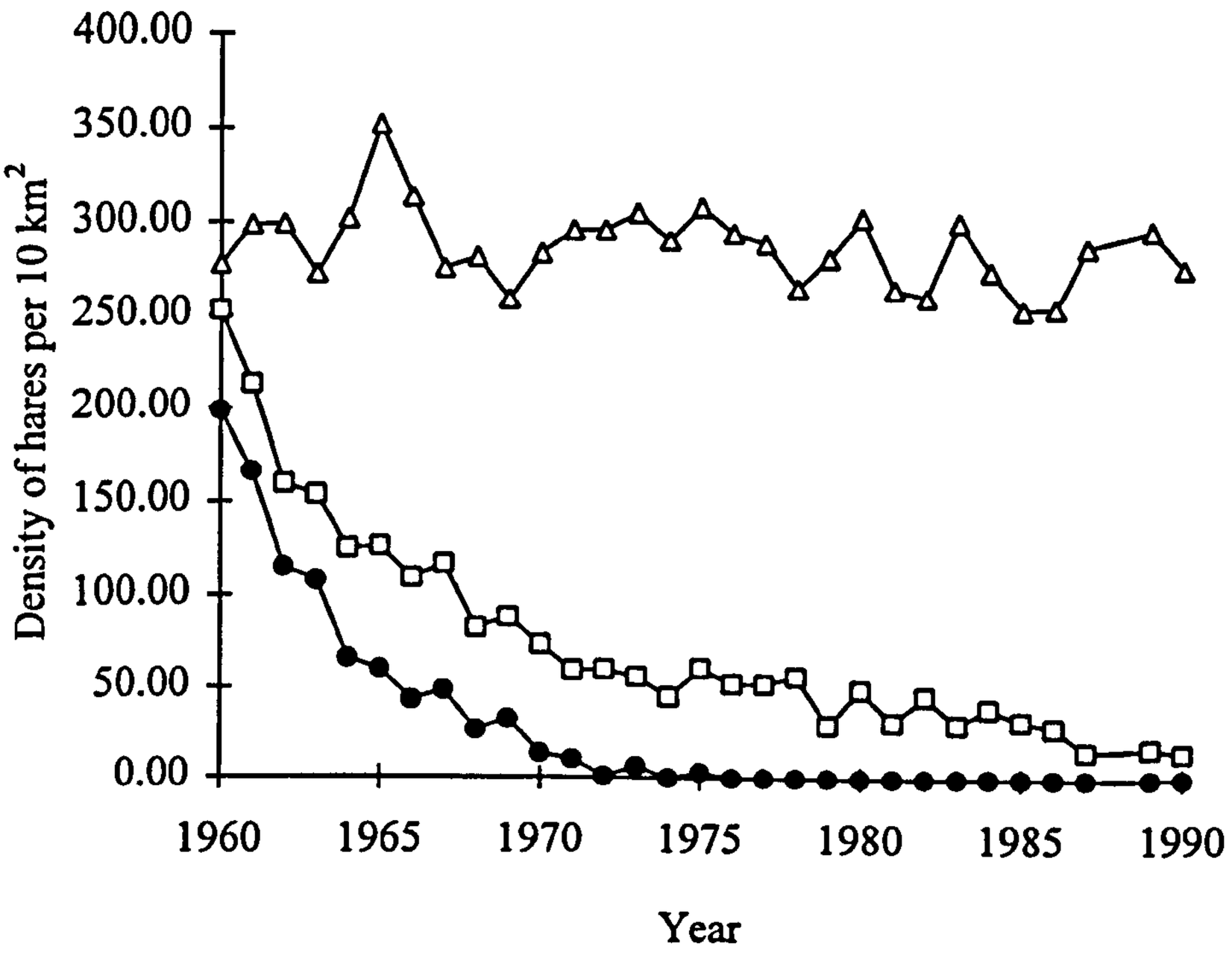


Figure 3.11. The effects of an annual cull on a closed population of hares. A cull that kills 10% of the adults each year is apparently sustainable (Δ), but cull which kills 25% (□) or 50% (•) drives the population towards extinction.



removed by shooting they do not breed in the year of their death. This still remains realistic, since animals are shot at the beginning of the breeding season, before they have had a chance to wean offspring. Therefore, February hare culls have important consequences for the hare population because they are held at a time when there are very few juveniles in the population, thus meaning that nearly all the animals that are shot would have gone on to breed in that year. This contrast with autumn shoots that are sometimes held, which kill large numbers of juveniles born earlier in the year, many of which would presumably have died anyway, prior to breeding.

3.4 Discussion

Hare populations proved to be extremely sensitive to changes in recruitment, caused either by reducing fecundity or leveret survivorship. This is the typical pattern found in short lived animals who invest a large amount of resources into reproduction (Flowerdew 1987). It was found that a 50% reduction in recruitment created similar declines in the model population that have occurred in the real East Anglia population (Tapper & Parsons 1986). This is remarkably consistent with the data in chapter two. The shape of the decline curves are also similar between the model and real data: sharp early declines followed by gradual decline. Notably, whilst an immediate reduction in recruitment of greater than 50% produced sharp declines in population size within the first five years of the simulation, gradual changes in fecundity and leveret survivorship produced less striking effects. However, grass diversity did decline rapidly in the early 1960s (see chapter two) and arable habitats were undergoing a rapid phase of intensification at this time (e.g. see O'connor & Shrubb 1986). These effects could also have been exacerbated by severely cold winters in 1961/2 and 1962/3 (Hutchings &

Harris 1996). Habitat change and cold winters could have combined to bring about large and sudden changes in the recruitment of hare populations. The reason that hare populations continued to decline in later years is because habitat change continued to reduce food resources in summer, and hence reduced recruitment.

The data in chapter two indicated that there was a less than 10% chance that any of the leverets born between March and June survived to the following February: the earliest possible age that they could breed. Since the majority of births occur in this period, the models in this chapter indicate that this would be sufficient to limit hare populations, but would not drive them to extinction. This also stresses the importance of births early in the season (January and February), which presumably act to buffer populations from further decline.

The results also indicated that a population that has undergone a decline, and that has a much lower level of recruitment, is far more unstable than a larger population with greater recruitment. The instability of low density hare populations may explain the large variation in density that is observed between some hare populations. These results also suggest that hare populations ought to fluctuate more now than earlier in the decline. However, this may not show up in game bags since areas chosen for hare shoots tend to be selected on the basis of high hare density, and also they may be cancelled if hare numbers are not thought to be high enough.

The results demonstrated that the adult age structure remained the same after changes in fecundity and leveret survivorship, but changed significantly with changes in adult survivorship. The age structure of current hare East Anglia populations is similar to that observed in the 1970s (Lincoln 1974), and similar to most other studies: there is

no indication of poorer than expected adult survivorship. Therefore, the evidence suggest that it is most likely that changes in recruitment (as a result of reduced fecundity, leveret survivorship, or both) have caused the decline of hare populations. In addition, when heavy adult mortality is applied, as a result of an annual cull, the populations go extinct very rapidly. The minimum estimate of the percentage of animals shot in an annual cull is 40% (Tapper & Stoate 1994), which would not be sustainable for a closed population. Where a cull occurs, therefore, large scale immigration must occur to buffer the population. Fortunately for brown hare populations, the area of culling tends to be small (none of the study areas in Chapter 2 covered an area greater than 5 km^2) and normally within estate boundaries, meaning that although small pockets of hares may be wiped out, surrounding areas within the estate will be unaffected.

Combined with the data from Chapter two, a more detailed hypothesis is formed: hare populations are limited by poor recruitment, which has most likely been brought about by reduced leveret survivorship, although possibly in combination with lowered fecundity . This has been brought about by habitat change which has reduced the availability of high quality summer forage, notably spring cereals and ley grass.

3.4.1 Conclusions

The low leveret survivorship found in chapter two is clearly sufficient to limit hare populations in East Anglia. However, sharp declines in hare numbers in the early 1960s are more likely to have been brought about by cold winters. The analysis also suggests that hare populations in the 1990s are stable, but at a higher risk of undergoing a

temporary decline than pre-decline populations. The brown hare is however, at no risk of going extinct in East Anglia if present conditions remain. Culling adults causes a severe population crash. Culled populations are likely to depend heavily on immigration for their survival. Also, relatively small areas are shot. The typical area shot for hares is normally no more than about 5km^2 (see table 2.3 page 30). The study populations from chapter two are likely to recover from immigration, although a study documenting this would be useful. Also, further work could concentrate on the timing of hare culls. The data in chapter two suggest that breeding during February is important in maintaining high hare densities. It is possible that later culls, such as the Autumn cull held in many European countries would have a different effect on hare population dynamics.

3.5 Summary

(1) A model hare population was created, using a Leslie matrix design. This combined data on age structure, fecundity and survivorship. These data were obtained from literature sources and from the data in chapter two.

(2) An initial, stable, pre-decline population was created, and then manipulated to determine the fecundity and survivorship changes required to make the population decline by 75% over 30 years: the same decline as has been observed in East Anglia.

(3) It was found that an overall reduction in annual recruitment of 50% was required to simulate the decline of hare numbers. When leveret survivorship or fecundity were

manipulated to reduce annual recruitment there were no significant effects on the age structures of the model populations.

(4) When adult survivorship was manipulated, there were significant effects on the age structures of the model populations. However, the data in chapter two did not show age structures that were atypical. Therefore it is concluded that changes in adult survivorship are unlikely to have caused the decline of hare populations.

(5) Changes to fecundity and leveret survivorship produced populations which declined in a similar manner to the real East Anglia population: rapid early declines followed by a gradual return to stability at lower densities. However, it remains likely that heavy population crashes in the early 1960s were brought about by cold weather.

(6) Hunting, was modelled by adding adult emigration from the population. Closed populations were found to be able to sustain only very low levels of hunting, and could not sustain he levels of hunting applied in a typical cull. It is hypothesised that where culling occurs, pockets of hares are almost entirely wiped out but are replaced by immigration from surrounding areas.

(7) The results of this chapter support the hypothesis that hare populations are limited by recruitment, and suggest that the reduced recruitment observed in chapter two would be sufficient to limit hare populations.

(8) In the next chapter, I examine patterns of fecundity and leveret survivorship in relation to the food resources available during winter and summer.

CHAPTER FOUR

THE NUTRITION OF BROWN HARES: THE EFFECTS OF SEASON AND SOCIAL STATUS

4.1 Introduction

An important feature of the analysis in chapters two and three was that although it was shown that recruitment was reduced, and that this was crucial in limiting hare populations, it was impossible to determine whether this was the result of reduced fecundity or leveret survivorship, or a combination of both. This chapter aims to assess the fecundity of females, and assess the chance of offspring survival, in relation to the food resources available to the female hare in winter and summer. Since fecundity and leveret survivorship were good in winter, the food-resource limitation hypothesis predicts that food should not be limiting at this time, whereas in summer food should limit fecundity or leveret survivorship, or both.

If food resources are limiting a population, then at a critical point of the year the food must be either used up, or become of such a low quality that it can no longer support the needs of the individual (Sinclair 1987). In order to determine whether this is the case, the diet requirements and availability must be established (for example see Sinclair 1987; Owen-Smith 1994). The requirements of individuals can be divided into ***maintenance***, which describes an animal which is neither depositing or using up body tissue, ***growth*** and ***reproductive*** costs. In mammals, these costs can either be measured by techniques such as respirometry or doubly labelled water (e.g. see Blaxter 1989) or by the use of allometric scaling.

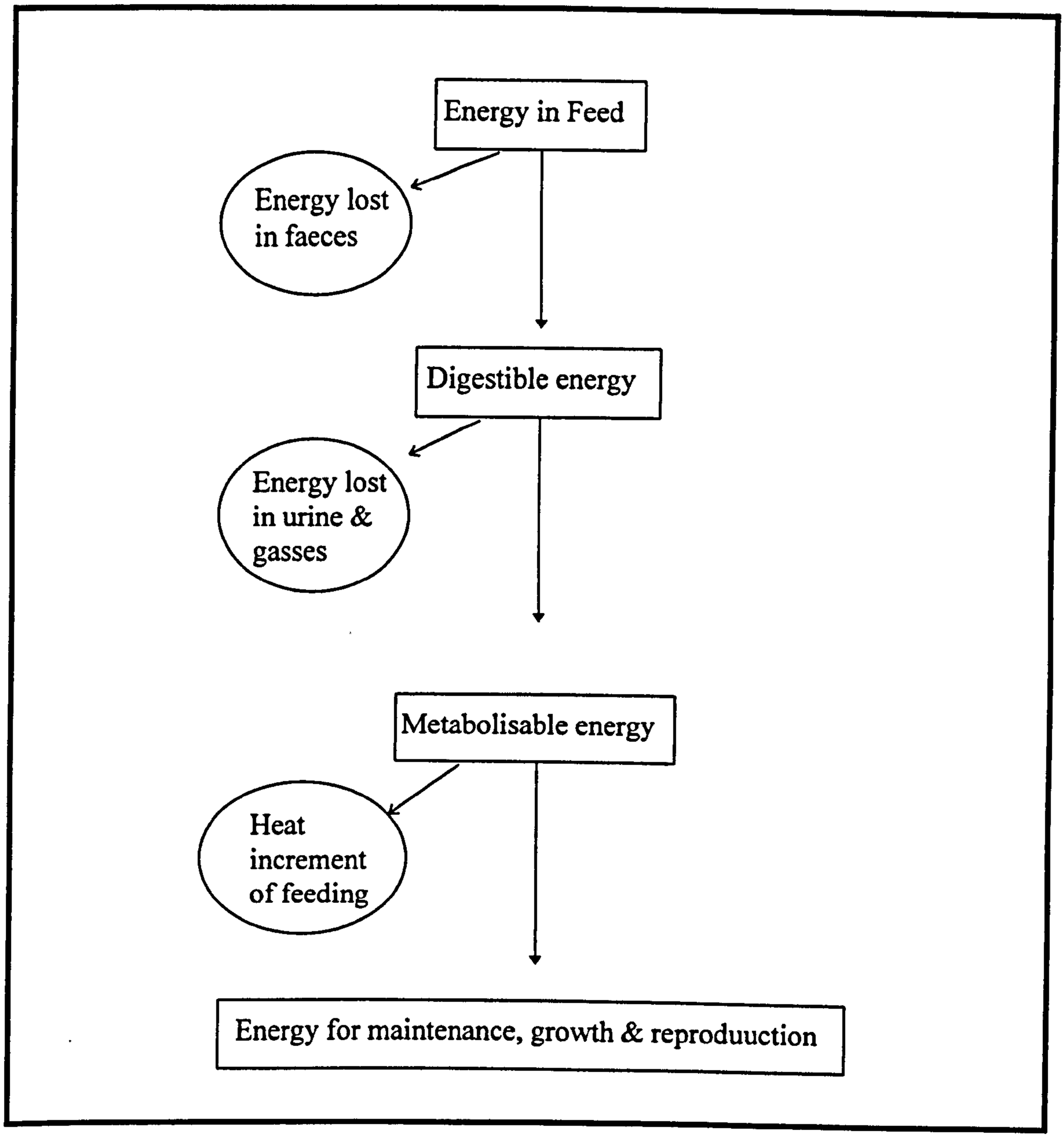
Allometric techniques scale costs to body weight. For example, Kleiber (1961) found that the basal metabolic rate (b.m.r.) of mammals was proportional to body weight to the power 0.75, and produce a constant 70 kcal of heat (292.99 kJ) per $kg^{0.75}$ per day. However, b.m.r is a medical term which describes the minimum energy requirements needed to sustain essential life processes (Louw 1993). It is therefore only of limited use, and a far more useful measure of energy expenditure is field metabolic rate (f.m.r) - the energy requirements of a free living mammal in its natural environment. Nagy (1987), using results obtained from doubly labelled water studies, found that the field metabolic rate was typically three times b.m.r., the increase being due to the costs of activity and posture. Therefore, if the body weight of a mammal is known both basal and field metabolic rates can be obtained. Basal metabolic rate has also been measured for *Lepus europaeus* (Kronfeld & Shkolnik 1996) in desert conditions, and *Lepus townsendii* (Rogowitz 1990) in temperate conditions. The work of Rogowitz (1990) showed that in temperate environments, *Lepus townsendii* increased their b.m.r. in winter to compensate for decreased environmental temperatures. Using equations given by Rogowitz (1990) and Kronfeld & Sholnik (1996), summer and winter b.m.r. can be estimated for brown hares and compared with the estimate given by Kleiber (1961).

The costs of growth and reproduction can then be added to the field metabolic rate. The most common measure of growth is the change in live-weight (McDonald, Edwards & Greenhalgh 1988), and this allows the cost of growth to be determined, if the body composition is known; this can be estimated from the cost of depositing fat and protein. Reproduction is divided into the cost of gestation and lactation.

Lactation is the more costly, and costs can be established if the composition and quantity of milk secreted is known (Webster 1988). Gestation costs can be measured from the growth rates of embryos in a similar way to post-natal growth. However, this cost represents only 10-15% of the total cost, the rest being the result of uterine, placental and mammary tissue production and maintenance (Gittleman & Thompson 1988).

Once the year round costs have been established, the energy and nutrients in the diet must be assessed, and also the ability of the animal to digest its diet. The pathway of energy through the mammal is summarised in Figure 4.1. For a realistic assessment of the energy available to the animal, the total energy of the feed must be known, as must the losses of energy in faeces, urine and gases. Also the heat increment of feeding must be estimated (HI); this is heat which is lost during the process of intake and digestion, and is of no use to the animal, except possibly in very cold environments (McDonald *et al.* 1988). Despite the fact that HI is not constant for all diets, it can be reasonably estimated for wild animals eating a typical diet. More importantly, HI increases as mammals deposit tissue or produce milk (as a result of heat loss during synthesis). Therefore, lactating, pregnant or growing animals will lose more energy to HI than other animals. However, the energy exchange has been widely studied in domestic animals (and is of great importance in animal production systems), and this information can be used to estimate HI under different conditions, as a wide range of domestic and non-domestic animals have been shown to be highly similar in terms of energy exchange efficiency (Webster 1988).

Figure 4.1 The pathway of energy through the mammal (from McDonald, Edwards & Greenhalgh 1988).



The requirements for nutrients are normally expressed as g/kg in feed (e.g. see Church 1990). Some nutrient types may not be equally digestible in all feeds, for example protein, and therefore may be expressed as g digestible / kg of feed (e.g. see Church 1990). The nutrient requirements of most domestic species have been established and are widely available. These provide baseline figures for wild species, although in domestic situations, the pressures to produce quickly means that higher quality diets may be used than are available to comparable wild species.

A wide range of diet studies have also been carried out on the rabbit (*Oryctolagus cuniculus*), which is an important meat and fur animal in some countries (Santoma *et al.* 1989; Church 1990). Rabbits and hares have similar digestive systems: they are hindgut fermenters, meaning that fermentation of digesta occurs in the large caecum. However, such small herbivores require a relatively greater flow of nutrient and energy per unit body mass than larger species (Santoma *et al.* 1989). In order to achieve this, hindgut fermenters have developed a mechanism which selectively retains easily digestible feed particles in the caecum, but allows larger less digestible fractions to be passed towards the anus and excreted as hard faeces (Santoma *et al.* 1989). After initial microbial breakdown, caecal material is passed in soft pellet form towards the anus and is re-ingested. A mucosal cover protects the pellets from digestive attack in the stomach, and allows microbial action to continue (Santoma *et al.* 1989). This mechanism allows a high intake rate and a rapid, efficient breakdown of digestible material. Clearly, rabbits and hares are adapted to take advantage of the easily digestible, high energy components of feed and have the ability to process large quantities. However, they are therefore

susceptible to changes in diet quality. For example, rabbits are much poorer in their ability to digest cell wall constituents than larger herbivores (Santoma *et al.* 1989), which normally increase as a component of grass as it matures (Van Soest 1994). Generally, as a herbivore increases in size, and therefore as its requirements per unit body mass decrease, it can include an increasing amount of poor quality forage in the diet, even though it takes longer to digest. This lead Van Soest (1994) to conclude that herbivores over 40 kg do not have to be selective feeders: thus a three or four kg brown hare must be highly selective in choosing its diet.

For herbivores, diet quality is most commonly expressed in terms of nitrogen (protein), energy and digestibility, since these parameters are relatively straightforward to determine and are of great importance to the nutrition of the animal. Other components of the feed, such as fats, tend to be less important, unless they are at abnormally low levels. In the case of fat, dietary fat makes only a small contribution when compared to the large amount of volatile fatty acids produced during the process of fermentation. This chapter therefore examines the nitrogen and energy exchange in hares, using estimates of requirements based on literature data, and the direct measurement of the digestible energy and nitrogen in the diet. For hares, this represents the first attempt to identify and quantify the direct consequences of habitat change on diet and energy and nitrogen balance.

4.2 Methods

4.2.1. The collection of samples

Samples of hares were obtained from February culls in 1992 (see chapter 2) and from later culls between April and June from the East Anglia region in 1993 and 1994 (Table 4.1). The difficulty of finding hares after February meant that sample sizes were low, and that hares were shot either in commercial forestry or in crops such as sugar beet. All hares were examined post-mortem, the methods of which are given in chapter two. For the purposes of diet analysis, the samples were categorised by season (February as winter, April to June as Summer), then split by sex. The females were then categorised as breeding (pregnant or lactating) and non-breeding. Males were split into above and below mean carcass weight. The social status of males is thought to be related to body weight, such that heavier males are higher in the dominance rank (Holley & Grenwood 1984); by splitting males in this way, the effect of the dominance system on diet could be examined.

Stomachs were removed and weighed full and empty, and the contents stored frozen for later analysis. Faecal pellets were taken from the end of the digestive tract. Brown hares are ceacotrophs, and therefore, care was taken to determine if the pellets were soft first stage pellets (once round the digestive tract) or hard final stage pellets (twice round the digestive tract). Only final stage pellets were used in the analysis, since they represent the indigestible fractions of the diet. All stomach and faecal samples were freeze dried and ground using a pestle and mortar prior to analysis. The species composition of the diet of the summer animals was also

Table 4.1 A comparison of summer and winter cull samples

Adult Females	mean carcass weight, kg	mean hind foot length, mm	mean body length, cm	mode kidney fat index
February cull† n=293	3.07±0.01	132 ±0.4	62.6±0.1	2.00
April-May culls‡ n=42	2.93±0.46	132 ±0.8	60.6±0.5	1.00

Adult males	mean carcass weight . kg	mean hind foot length. mm	mean body length, cm	mods kidney fat index
February cull† n=287	2.87±0.02	132 ±0.4	62.2±0.1	2.00
April-May culls‡ n=72	2.56±0.61	130 ±0.1	59.9±1.0	1.00

Females	mean number of foetus	% pregnant	comparable figures from Lincoln (1974)	
February cull† n=293	1.0	54.2	mean number of foetus 1.0	%pregnant 60
April-June culls‡ n=42	1.9	61.7	mean number of foetus 3.0	%pregnant 100

† This sample is referred to in the text as the 'winter sample'; ‡ this sample is referred to in the text as the 'summer sample'
Adult animals are defined as all those over 2.0 kg (see text).

estimated, using the same technique which was used on the winter samples. The method for estimating species composition is described in chapter two.

4.2.2 Measuring food intake and faecal output

Food intake can be measured in live animals either by direct observation or by indirect marker techniques (Van Soest 1994). However, neither of these technique can be applied to a cull sample. Two alternative techniques were used here to estimate intake. In the first the amount of food in the caecum is measured, and combined with the retention time of food the caecum, is used to estimate of intake. The caecum represents the slowest stage of digestion, and therefore limits intake. If c = caecal contents, r = retention time in hours and d = the digestible fraction of the diet, then the total amount of food that passes through the caecum (Tc) is:

$$Tc = (c \times 24/ r)$$

and the total intake, taking into account the digestibility of the diet is

$$24 \text{ hour intake} = (Tc / d)$$

Digestibility is included to take account of the fact that some of the diet does not enter the caecum but is expelled, and this method therefore assumes that all digestible food enters the caecum. Retention time was estimated as 12 hours, based on the estimate for the rabbit (Santoma *et al.* 1989). However, retention time is not constant for all diets, and tends to be slower with less digestible diets (Van Soest 1994). Therefore, to provide a second estimate of intake, the relationship between body size and food intake found by Nagy (1987) was applied to the brown hare. Therefore although food intake cannot be measured directly for this sample, realistic estimates can be made.

Faecal output was measured by using the indigestible marker technique (Van Soest 1994). This involves measuring the concentration of an indigestible component of the feed which is compared with the concentration in the faeces. The ratio was then used to work out how much of the feed is digested, thus if X represents the concentration of indigestible marker:

$$\% \text{ digestibility} = X_{feed} / X_{faeces}$$

The most common component of feed used to estimate digestibility is lignin (Van Soest 1994), which was also used in this study. The percentage of lignin in the samples was determined by the acid-detergent method (Van Soest 1994). Samples of freeze dried faeces and stomach contents were weighed to the nearest 0.0001g and then boiled in an acid detergent solution for one hour. The remaining solids (containing lignin) were then filtered from the solution and placed in 25% sulphuric acid for three hours, leaving behind only solids containing lignin and minerals. These were dried at 100°C and weighed (to the nearest 0.0001g), and the remaining lignin removed by further drying at 600°C for 12 hours. The weight of the minerals was then measured (to the nearest 0.0001g). This value was subtracted from the weight of the sample with minerals and lignin, giving the weight of lignin. This value was then converted into a percentage of the original weight of the sample.

4.2.3 Measuring heat increment and urine losses

Heat increment (HI) is the measurable rise in body temperature of a mammal after it has eaten. HI represents waste heat lost during intake and digestion and has been the subject of a considerable amount of research (e.g. see Webster 1988). Estimated values have been obtained for domestic species under a variety of conditions, but are

similar between species under normal conditions. Typically, herbivores lose between 20 and 30% of their metabolisable energy intake (ME) as HI (Blaxter 1989). Therefore, at maintenance, an average value of 25% of ME lost as HI is used in this analysis. For a growing, pregnant or lactating herbivore, HI increases to between 30 and 50% of ME (Blaxter 1989). Given the wider variance of this measurement, it was decided to use the estimate given for the rabbit, at 35% of ME lost as HI, for growing, lactating or pregnant animals.

Urine losses are much less variable between species, and do not vary with the condition of the animal (Blaxter 1989). A typical value for urine losses of 5% of digestible energy intake is used in this analysis.

4.2.4 Measuring nitrogen and energy in food and faeces

Samples of stomach contents and faeces were weighed to the nearest 0.0001g, and their nitrogen content measured directly in a nitrogen autoanalyser. Bomb calorimetry was used to calculate the gross energy of the food and faeces. In this method, samples of known weight (to the nearest 0.0001g) were placed in a bomb calorimeter and the energy content evaluated after complete oxidation of the sample. The amount of nitrogen and energy in the diet was then multiplied by the digestibility of the diet, to give the digestible nitrogen and energy that is available to the animal.

4.2.5 Estimating energy and nitrogen requirements

The basal metabolic rate of several *Lepus* species, including the brown hare have been calculated. Some of these results were examined by Rogowitz (1990). The oxygen consumption of a resting hare was found to be:

$$\log \text{ml } O_2/\text{ hour} = 0.43 + 0.79(\log \text{mass, g}) \text{ in summer}$$

and

$$\log \text{ml } O_2/\text{ hour} = 0.57 + 0.77(\log \text{mass, g}) \text{ in winter}$$

The summer estimate was not significantly different from the Kleiber equation (Rogowitz 1990), whereas the winter equation was significantly higher. Given that 1ml of O_2 is equal to 20.083 joules, this gives an estimated b.m.r. of:

$$\text{winter b.m.r.} = 220 \text{ kJ/kg/day} \pm 6.0$$

$$\text{summer b.m.r.} = 270 \text{ kJ/kg/day} \pm 5.0$$

Oxygen consumption in brown hares has also been estimated Kronfeld & Shkolnik (1996). For normal hares, of mean weight 2.8 kg, this was estimated to be:

$$O_2 \text{ consumption} = 0.54 \pm 0.071 \text{ ml/g/hour}$$

This value is very similar to that predicted by Rogowitz (1990) for a 2.8 kg animal in summer, which is 0.51 ml/g/hour. Given the close estimates of b.m.r., it was assumed that in summer b.m.r. = 220± 5 kJ/kg/day and 270± 6 kJ/kg/day in winter. The standard error of these estimates (2%) were based on the standard errors given by Rogowitz (1990) and were also used produce standard errors of f.m.r. F.m.r. was calculated as 3 × b.m.r (Nagy 1987). For the analysis, it is assumed that hares do increase their basal metabolic rate in winter, and therefore also their field metabolic rate. Thus, it can be determined if such an increase is realistic, and also its

consequences for the growth and reproduction of hares at this time. The estimates of b.m.r. and f.m.r. in winter and summer are given in Table 4.1.

The nitrogen requirements of hares were estimated from those of rabbits, which are often expressed in terms of protein, although protein is almost exclusively measured as nitrogen × 6.25. Thus nitrogen and protein are inter-changeable. However, most authors present their data as protein, even though they actually measure nitrogen. The minimum percentage digestible protein (DP) is can be calculated from the digestible energy content of the diet (gross energy of the diet minus energy lost in faeces), and this has been estimated for an animal at maintenance as:

Minimum DP =DE (kJ/kg)/59.7 (Church 1990)

For a growing, pregnant or lactating animal, minimum digestible protein is given as:

Minimum DP =DE (kJ/kg)/47.8 (Church 1990)

Minimum DP is converted to minimum nitrogen by dividing DP by 6.25. In addition, Santoma *et al.* (1989) suggest that rabbits should have a minimum level of protein of 13% of the dry matter of the diet (or 2.1% digestible nitrogen). For the rest of the analysis, digestible nitrogen will be used, rather than protein, since nitrogen is measured directly and, as Macdonald *et al.*(1988) point out, it avoids making an unnecessary assumption that protein always equals nitrogen × 6.25.

4.2.6 Modelling energy and nitrogen exchange (i): maintenance

Maintenance is defined as the situation when an adult animal neither gains or loses energy: it is neither starving or depositing tissue (Webster 1988). In this model, this represents a non-breeding adult animal. If the model predicts that the metabolisable

energy available to the animal is less than maintenance, the animal is starving: if it is greater then the animal is retaining energy for growth or reproduction.

The model is based on Figure 4.1, and was built using Microsoft Excel which combined the energetic and diet data. The energy and nitrogen in the initial diet was converted to digestible energy, by removing the total energy and nitrogen lost in the faeces. Digestible energy was then converted to metabolisable energy by removing the energy lost in urine. The model allowed for intake, food quality and food requirements to be varied. The model also allowed for body weight, reproductive status (number of embryos and number of offspring lactating) and growth costs to be entered. The model was then run for winter and summer, and included the increased winter b.m.r. The results presented here, are for an animal of 3.5 kg, and represent an 'average' hare.

Energy gains were determined by taking the gross energy of the diet (energy in stomach contents × intake) and subtracting the losses described in Figure 4.1 (faecal and urine losses, and heat increment). The data used in this part of the model were taken from the diet analysis described above. In this model, intake was variable and urine losses were estimated from Blaxter (1989). The energy gains were then matched to the energy requirements, and the intake required for gains to be greater than requirements was calculated. This allowed a comparison with realistic estimates of intake.

For nitrogen the calculation is easier. It is assumed that the daily requirements of an adult animal at maintenance is equal to:

(DE (kJ/kg)/59.7)/6.25 (see section 4.2.5).

The amount of nitrogen in the diet is then multiplied by the digestibility of the diet, to give the remaining digestible nitrogen.

4.2.7 Modelling energy and nitrogen exchange (ii): gestation

This model is the same as that for maintenance only with the added costs of gestation and the associated change in HI (see section 4.2.3). The growth rate of the hare embryo is given by Broekhuizen & Martinet (1979). This is then multiplied by the energy content of embryo tissue, which is estimated to be 5kJ (Blaxter 1989). This cost is assumed to be 12% of the total cost of gestation (Blaxter 1989; Gittleman & Thompson 1988). The nitrogen required for gestation is estimated as :

DE (kJ/kg)/ 47.8)/6.25 (see section 4.25).

For the winter model, it was assumed that there was only one foetus, whilst in the summer model it was assumed that there were three. This is consistent with the typical litter sizes found at these times (chapter two; Lincoln 1974).

4.2.8 Modelling energy and nitrogen exchange (iii): lactation

The costs of lactation were modelled using the model for maintenance with the added costs of lactation, and increase in HI. The amount of milk produced by a lactating hare is given by Martinet & Demarne (1984). The energy content of the milk is 13kJ/kg. Using the figures for peak milk production for different litter sizes given by Martinet & Demarne (1984), the energy secreted daily in milk is 385kJ for one offspring, 616 kJ for two and 847kJ for three. As with gestation, the heat increment of lactating animals is greater, since heat is lost during milk production.

The nitrogen required for lactation is estimated in two ways. As with gestation, the value can be estimated from the DE value of the diet (see above). However, to provide a comparison, it can also be estimated from the nitrogen content of milk, given by Martinet & Demarne (1984), which is 16g N/kg milk. This can be added to the maintenance requirements to give a second, comparable estimate.

As with gestation, for the winter model it was assumed that there was only one offspring, whilst in the summer model it was assumed that there were three (chapter two; Lincoln 1974).

4.2.9 Modelling energy and nitrogen exchange (iv): growth

After a lactation of about 30 days, young hares continue to grow, and Flux & Angermann (1990) state that young animals grow at a rate of 19g per day until three months old. The cost of depositing this tissue is estimated to be 5 kJ/kg (Blaxter 1989). Associated with the deposition of tissue is an increased HI, such that 35% of ME is lost (see section 4.2.3). The mass specific basal and field metabolic rates were assumed to be the same as those for adults, and therefore, for this model, there were both winter and summer simulations, with winter animals having the increased b.m.r. and f.m.r. Juvenile *Lepus townsendii* were found to have increased metabolism at air temperatures $< 10^{\circ}C$ (Rogowitz 1990), but also a higher mass specific basal metabolic rate below 54 days of age. Therefore, metabolic rate may be slightly under-estimated in this model, for animals under 54 days. The requirements of nitrogen during growth were estimated as (DE (kJ/kg)/47.8)/6.25 (see section 4.2.5).

The model used here was the same as that used above, with the added costs of growth and HI. However, no cull data were available from juvenile animals, and it

was assumed that the diet that was available to adults, was also available to juveniles, for both winter and summer.

4.3 Results

4.3.1. A comparison of the samples

The details of the samples used in the analysis are given in Table 4.1, together with a comparison of literature data. There were several significant differences between those adult animals (>2.0 kg) shot in summer and those in winter. Summer breeding females had significantly lower carcass weights than winter breeding females (t-test, DF=178, t=-1.75, $p<0.05$) but had similar levels of kidney fat (Mann- Whitney U test, n=180, z=-1.5, N.S.). The summer females also had fewer foetuses than found in previous studies and the number of females lactating was low (Table 4.1). Also unlike winter, there was no significant increase in carcass weight with increasing numbers of foetuses (n=42, r^2=0.004, N.S.). In females with two foetus, mean winter carcass weight was 3.27 kg, but was significantly lighter at 2.87 kg in summer (t-test, t=3.53, DF=34, $p<0.05$). The seasonal difference was even greater when females with three foetus were considered, with mean winter carcass weight of 3.44 kg, compared to 3.05 kg in summer (t=3.79, DF=13, $p<0.01$). With non-breeding females, there was no significant difference between winter and summer carcass weights (t-test, DF=146, t=-0.39, N.S.) and also no difference in kidney fat (Mann-Whitney U test, n=155, z=-0.5, N.S.). However, males were significantly lighter in summer than in winter (t-test, DF=350, t=-5.23, $p<0.001$) and had less kidney fat (Mann- Whitney U test, n=365, z=-2.66, $p<0.01$).

4.3.2 The intake and output of feed by hares: the effect of season and social status

The species composition of the summer animals proved to be similar to the winter samples, with grasses comprising 78% of the diet, the remainder being largely forbs which comprised 18% of the diet. As with the winter samples, the grasses were difficult to identify to the species level.

The weight of the stomach contents was not significantly different between breeding females in winter and summer (t-test, t=1.59, DF=150, N.S.), nor different between non-breeding females (t-test, t=1.61, DF=150, N.S.), or males (t-test, t=2.05., DF=294, N.S.).

The weight of the caecum showed similar patterns, with no significant differences emerging between winter and summer (t-test, t=1.90, DF=55, N.S.), although sample sizes from summer were low, since the caecum is large and was frequently suffered damage by shooting . An analysis between social groups was therefore not carried out. The range of values for the caecum was between 100 and 200g wet weight. Assuming a retention time of 12hrs in the caecum (Santoma *et al.* 1989), and a constant 200g in the caecum, this gives an estimated intake into the caecum of 400g per day (wet weight). However, only the easily digestible fraction enters the caecum. Intake rate is therefore dependent on the digestibility of the diet, which is estimated in section 4.3.4. The estimated intake for a 4.0 kg hare, given by the allometric equation by Nagy (1987), is approximately 200g dry matter per day.

4.3.3 The diet of hares: the effect of season and social status

Within the summer sample, there was no significant variation in the nitrogen levels of the stomach contents (Table 4.2, ANOVA, DF=5,38, F=1.74, N.S.). However, there was significant variation within the winter sample (ANOVA, DF=5,68, F=7.0, $p<0.05$). and this proved to be caused by below mean weight males having a significantly lower nitrogen content in the stomach contents (Tukey test, $p<0.05$). Using the combined data sets from winter and summer, there was a significantly greater nitrogen content in the winter stomach contents, (t-test, t= 3.11, DF=92, $p<0.05$). The energy content of the diet also showed seasonal trends (Table 4.2), and was significantly higher in summer animals than winter ones (t-test, t=2.56, DF=126, $p<0.05$).

For the faecal analysis, only breeding females were used, since this provided an adequate data set for comparison of winter and summer and also provided data for modelling the cost of reproduction. There was no significant difference in the nitrogen content of the faeces between summer and winter (t-test, t=6.36, DF=48, N.S.). However, there were significantly higher amounts of energy in the faeces of summer breeding females (t-test, t=2.56, DF=48, $p<0.05$).

4.3.4 The lignin content and digestibility of the diet: the consequences for intake

There was a significantly higher lignin content in the stomach contents of summer breeding animals than winter ones (t-test, t=-3.32, DF=48, $p<0.05$, Table 4.2). Accordingly, there was also a higher concentration in the faeces of summer breeders (t-test, t=-2.98, DF=48, $p<0.05$).

Table 4.2 The energy, nitrogen and lignin content of the diet of hares in winter and summer. The figures represent the means with the standard error in brackets.

	Stomach contents		
	energy kJ/kg	% digestible nitrogen	% lignin
Summer			
breeding females n=25	19.7 (0.3)	3.4 (0.3)	5.1 (0.2)
non-breeding females n= 12	19.5 (0.2)	3.3 (0.4)	-
heavy males n= 10	19.3 (0.3)	3.3 (0.7)	-
light males n= 9	19.5 (0.2)	3.3 (0.2)	-
means	19.5 (0.3)	3.3 (0.3)	5.1 (0.2)
Winter			
breeding females n=25	18.5 (0.4)	4.6 (0.2)	3.0 (0.2)
non-breeding females n=25	18.2 (0.3)	4.5 (0.2)	-
heavy males n=10	18.1 (0.3)	4.4 (0.2)	-
light males n=10	17.9 (0.2)	3.8 (0.4)	-
means	18.3 (0.3)	4.4 (0.2)	3.0 (0.2)

	Faeces		
	energy kJ/kg	% nitrogen	% lignin
Summer breeding females n=25	19.7 (0.30)	5.6 (0.21)	14.3 (1.7)
Winter breeding females n=25	18.5 (0.31)	5.8 (0.34)	10.6 (1.7)

Using the mean concentrations of lignin in the diet and faeces, the digestibility of the summer and winter diets were calculated as:

summer: 64± 3%

winter: 72± 2%

The digestibility of the diet affects the estimated intake. Given that an estimated 400g passes through the caecum each day, this means that to fill the caecum twice, a hare would have an estimated intake of 548g in summer and 487g in winter. Summer animals required an increased intake because their diet was less digestible. Given that typically 80-90% of plant material is water (Church 1990), this means that dry matter intake would be in the region of 50g per day. This is much lower than the expected figure given by Nagy (1987), and this is likely to be the result of the highly selective ceacum: clearly not all of the digestible diet enters the caecum. This means that for hares, a more detailed knowledge of how much enters the caecum is required before it can be used to estimate intake.

4.3.5 Balancing requirements and availability (i): maintenance

Maintenance requirements for a 3.5 kg hare (adult) were found to be 2310± 46 kJ per day in summer, with an estimated increase to 2835± 57 kJ per day in winter, due to an increase in winter b.m.r. To sustain this level of expenditure, given the energy content and digestibility of the summer and winter diets, would require an estimated 240± 6g dry matter intake in summer and 290± 5g in winter (Figure 4.2). Thus despite a more easily digestible diet in winter, an increased intake was still required to cover the increased costs of b.m.r. The diet was found to be most sensitive to

changes in digestibility (Figure 4.3), although changes in energy were also important (Figure 4.4).

The digestible energy of the diet was found to be 12.2 kJ/kg in summer, and 13.3 kJ in winter (Table 4.2). This meant that the digestible nitrogen required for maintenance was 1.8% and 2.1% in summer and winter respectively. This is similar to the estimate of Santoma *et al.* (1989) that digestible nitrogen should be a minimum of 2.1% of the diet. However, the observed levels of digestible nitrogen were well above this for both winter and summer (Table 4.2), being estimated at 4.7% in winter and 3.1% in summer.

4.3.6 Balancing requirements and availability(ii): gestation

The growth curve of the embryo during gestation is given in Figure 4.5. The growth and therefore, cost of the embryo is not constant but is an increasing function of the age of the embryo, and so the maximum cost of gestation is toward the end of gestation. Using the cost of producing an embryo as 5 kJ/g, this gives a maximum cost of 38 kJ for each embryo, assuming there is a constant investment in each embryo. This means that the maximum cost of gestation, for a 3.5 kg hare in winter, with one foetus was estimated to be 7400 kJ/day, although in summer, with a reduced b.m.r. the same female could have three foetuses for a maximum of 6700 kJ/day.

However, the model predicted that an intake of 340g is requires to sustain the cost of gestation in winter, whilst an intake of 370 g in summer is estimated to be

Figure 4.2 The food intake required to cover the cost of maintenance in winter (□) and summer (Δ). To maintain a positive energy balance requires a higher intake in winter than in summer.

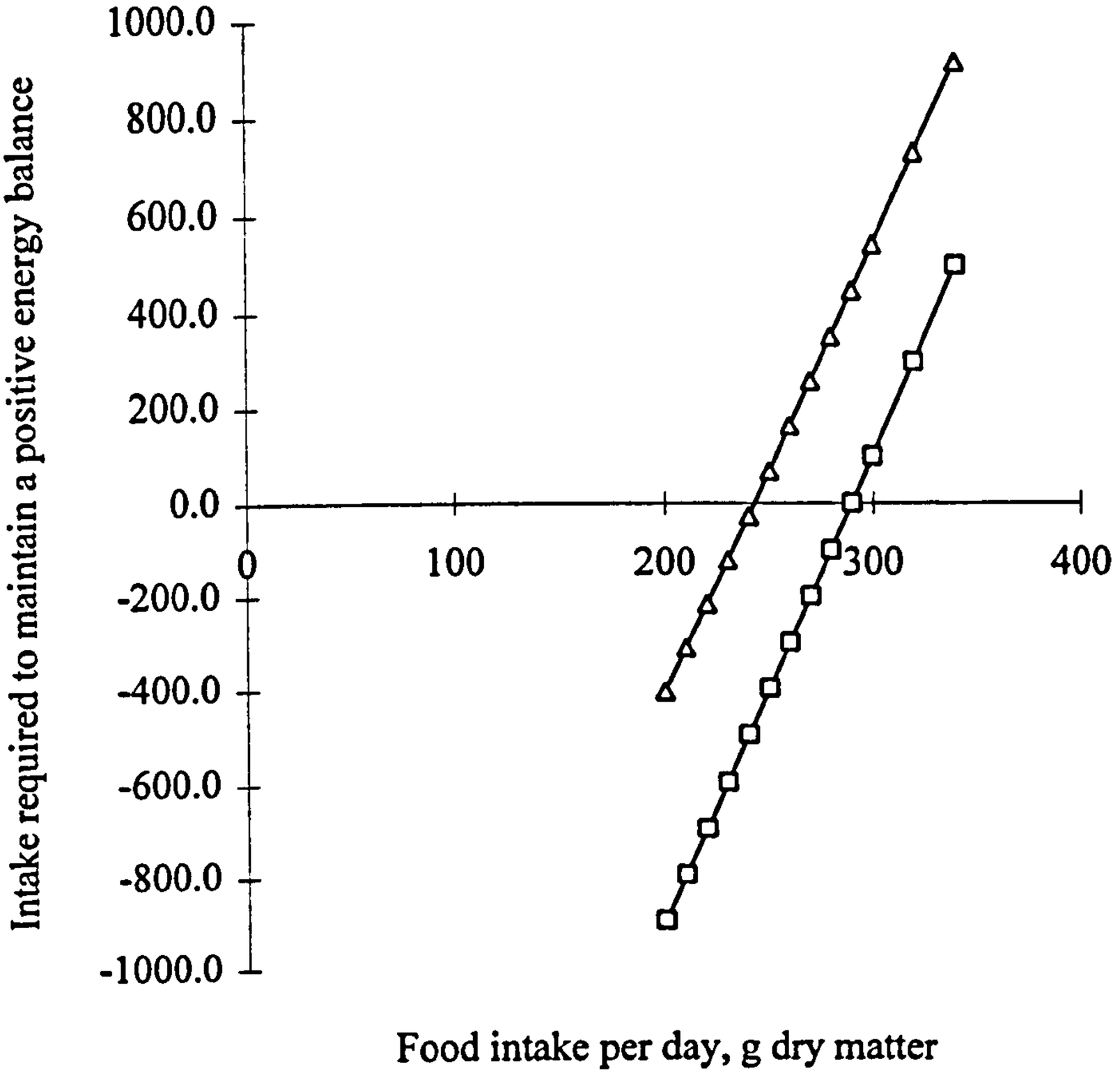


Figure 4.3 The food intake required to maintain a positive energy balance at maintenance, with the changing digestibility of the diet, for winter (□) and summer (Δ) animals.

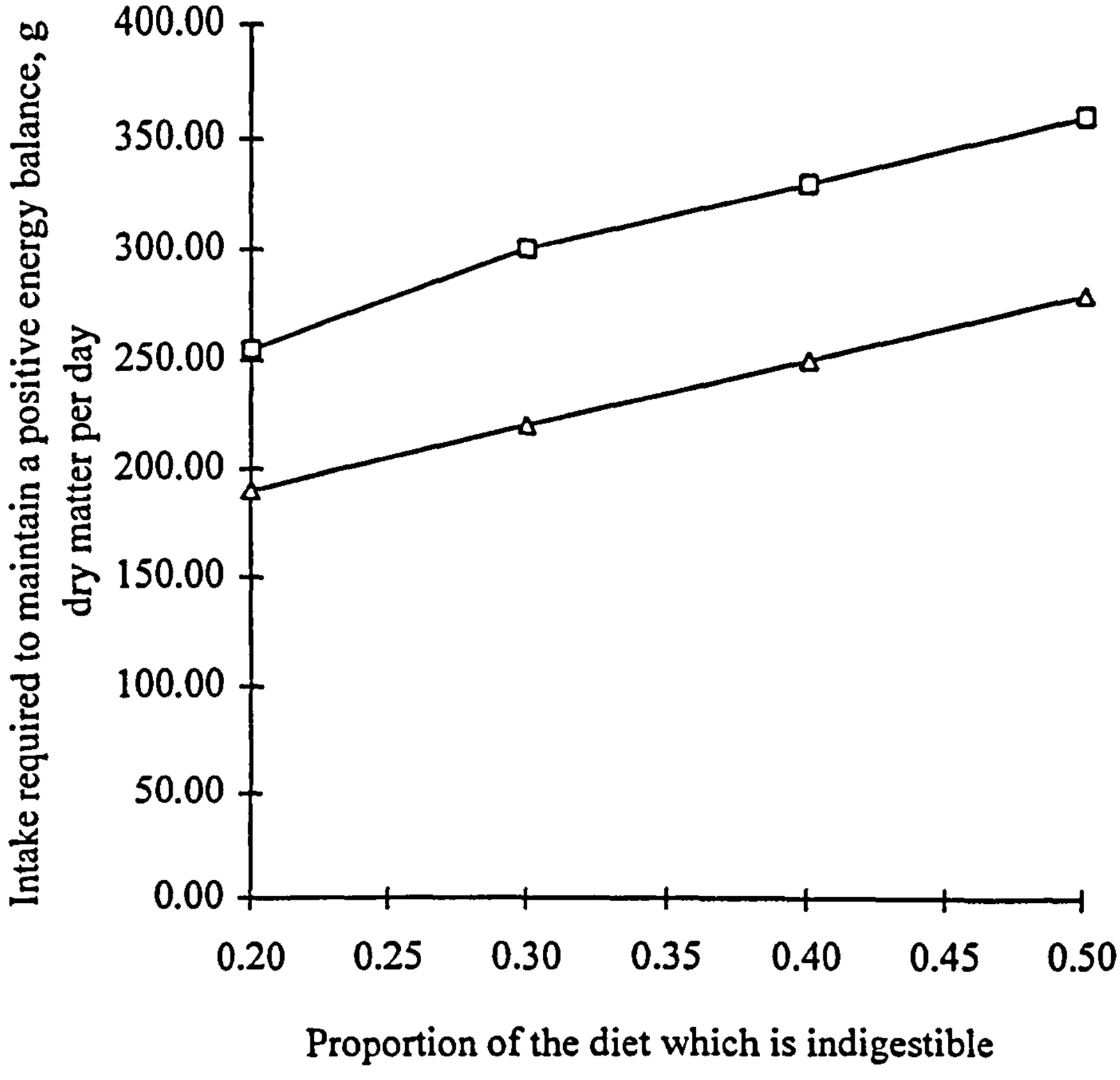


Figure 4.4 The food intake required to maintain a positive energy balance at maintenance, with the changing energy content of the diet, for winter (□) and summer (Δ) animals.

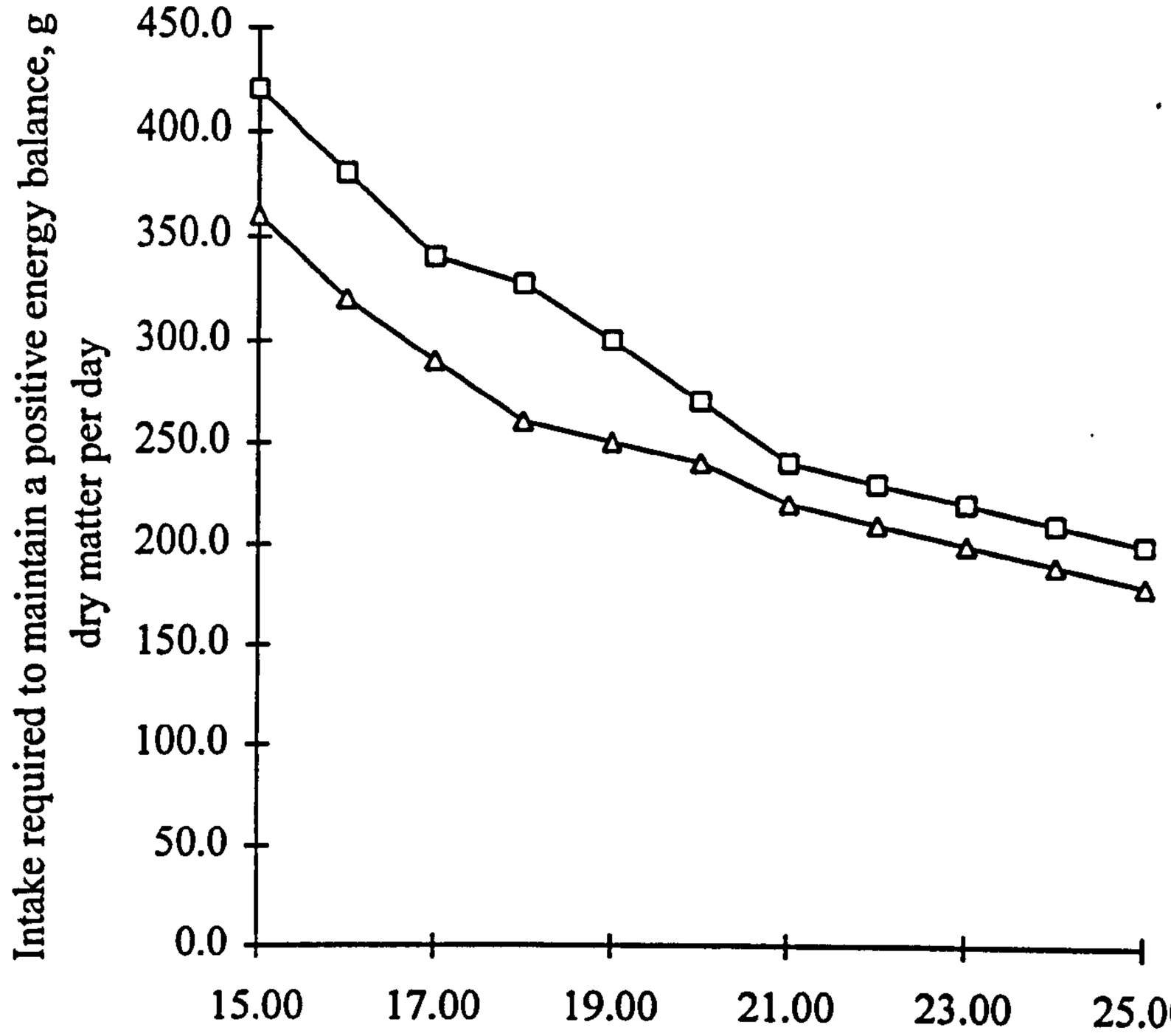
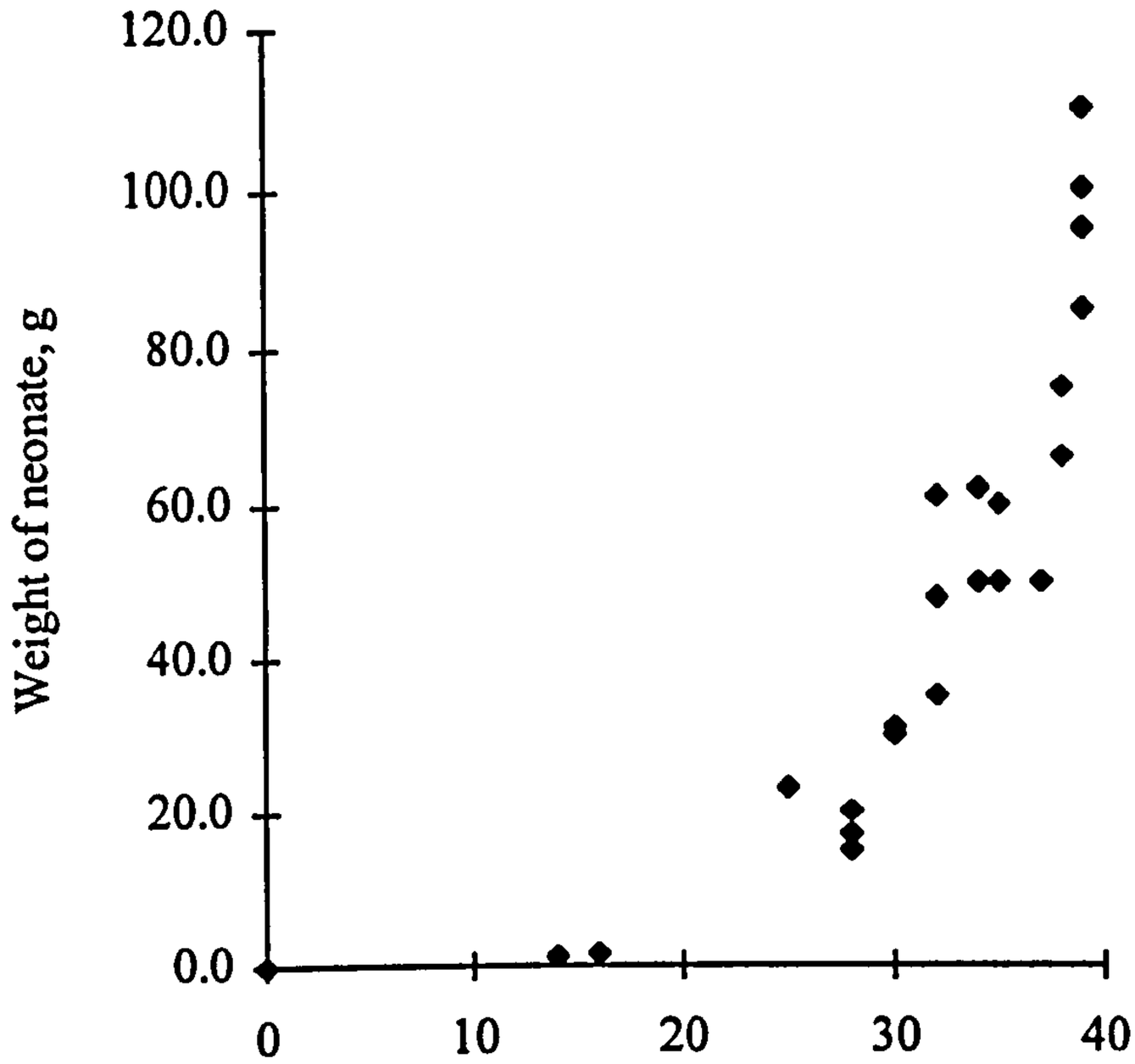


Figure 4.5 The growth of the embryo of *L. europaeus*. The graph is based on that given by Broekhuizen & Martinet (1979)



sufficient to cover the maximum costs associated with producing three offspring in summer (Figure 4.6). To produce each offspring after that requires an estimated 30g extra intake. The estimated nitrogen requirements for gestation was 3.0% and 2.1% in summer and winter respectively. As with maintenance, the observed levels of digestible nitrogen were sufficient to meet demands in both winter and summer (Table 4.2).

4.3.7 Balancing requirements and availability (iii): lactation

The cost of lactation is given in Figure 4.7. The cost of suckling one offspring in winter proved to be similar to the cost of suckling three in summer (winter, maximum cost 4240 kJ/day, summer 4076 kJ/day), with both requiring an estimated maximum intake of 350g. Note that in comparison with gestation, this level of intake must be sustained over a period of two weeks during peak lactation. The estimated nitrogen requirements for lactation were the same as those for gestation, and therefore, the observed levels of digestible nitrogen were sufficient (Table 4.2).

4.3.8 Balancing requirements and availability (iv): growth

The nitrogen requirement for growth is the same as that for gestation and lactation, and therefore the nitrogen in the diet available to the adult, would be sufficient to cover the costs of growth for juveniles. As a result of increased b.m.r., the cost of growth in winter was greater than the cost in summer, and required an increased intake (Figure 4.8).

Figure 4.6 The food intake required to cover the cost of gestation in winter (□) and summer (Δ). This figure indicates that at intakes above 340g in winter, and 370g in summer, there is a positive energy balance, and therefore enough energy to cover the cost of gestation.

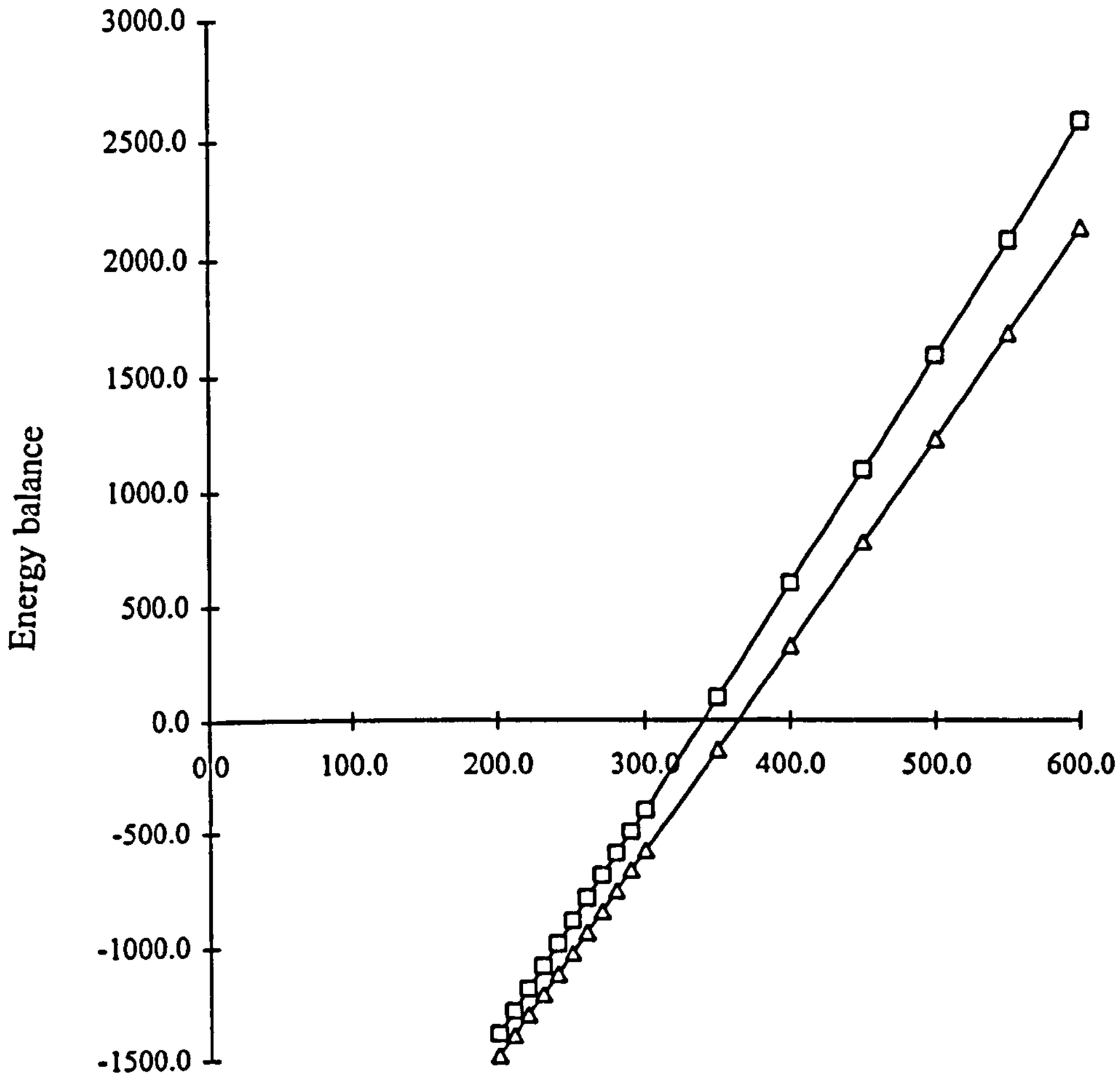


Figure 4.7 The food intake required to cover the cost of lactation in winter (□) and summer (Δ). This figure indicates that at intakes above 370g in both winter, and summer, there is a positive energy balance, and therefore enough energy to cover the cost of lactation.

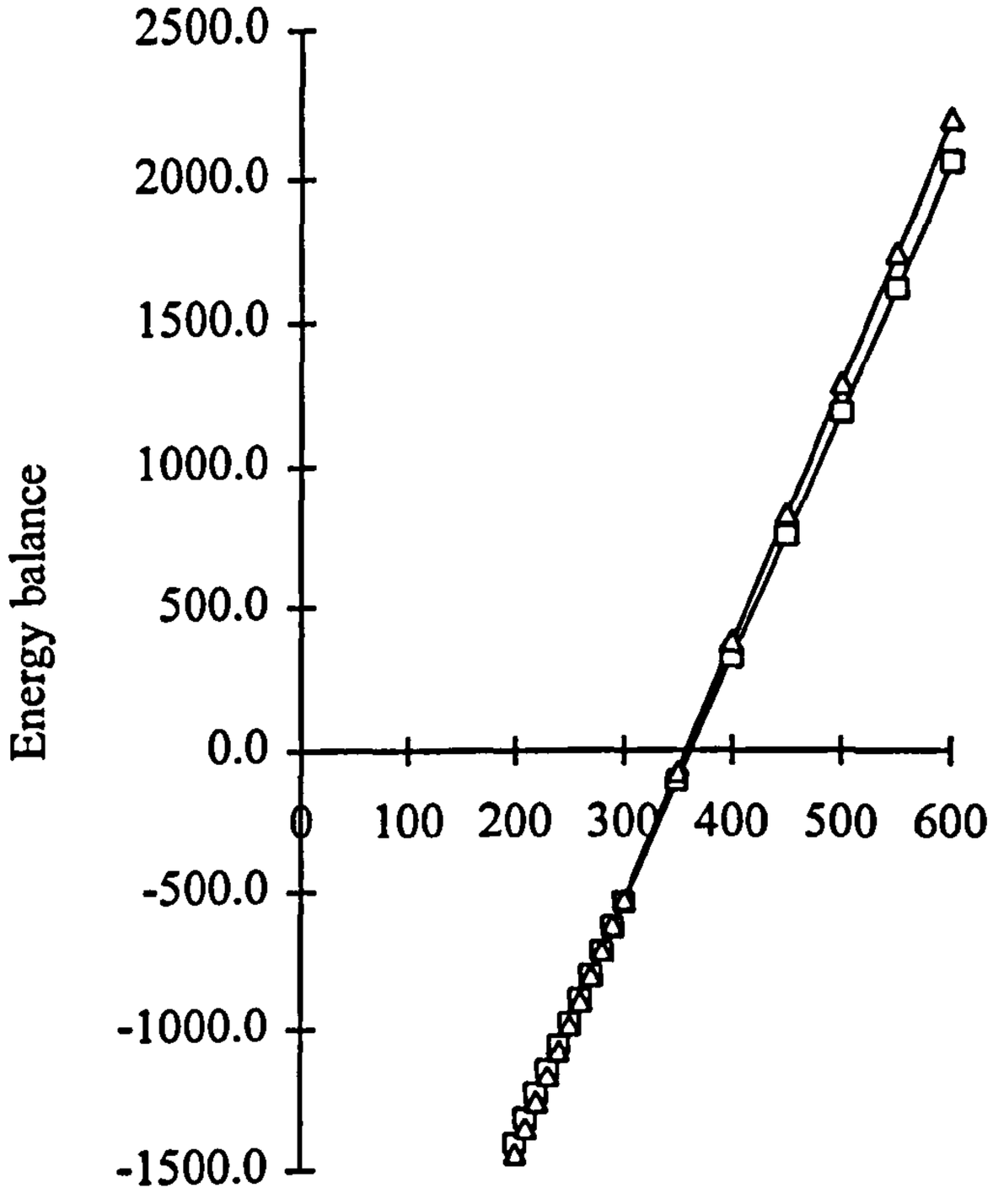
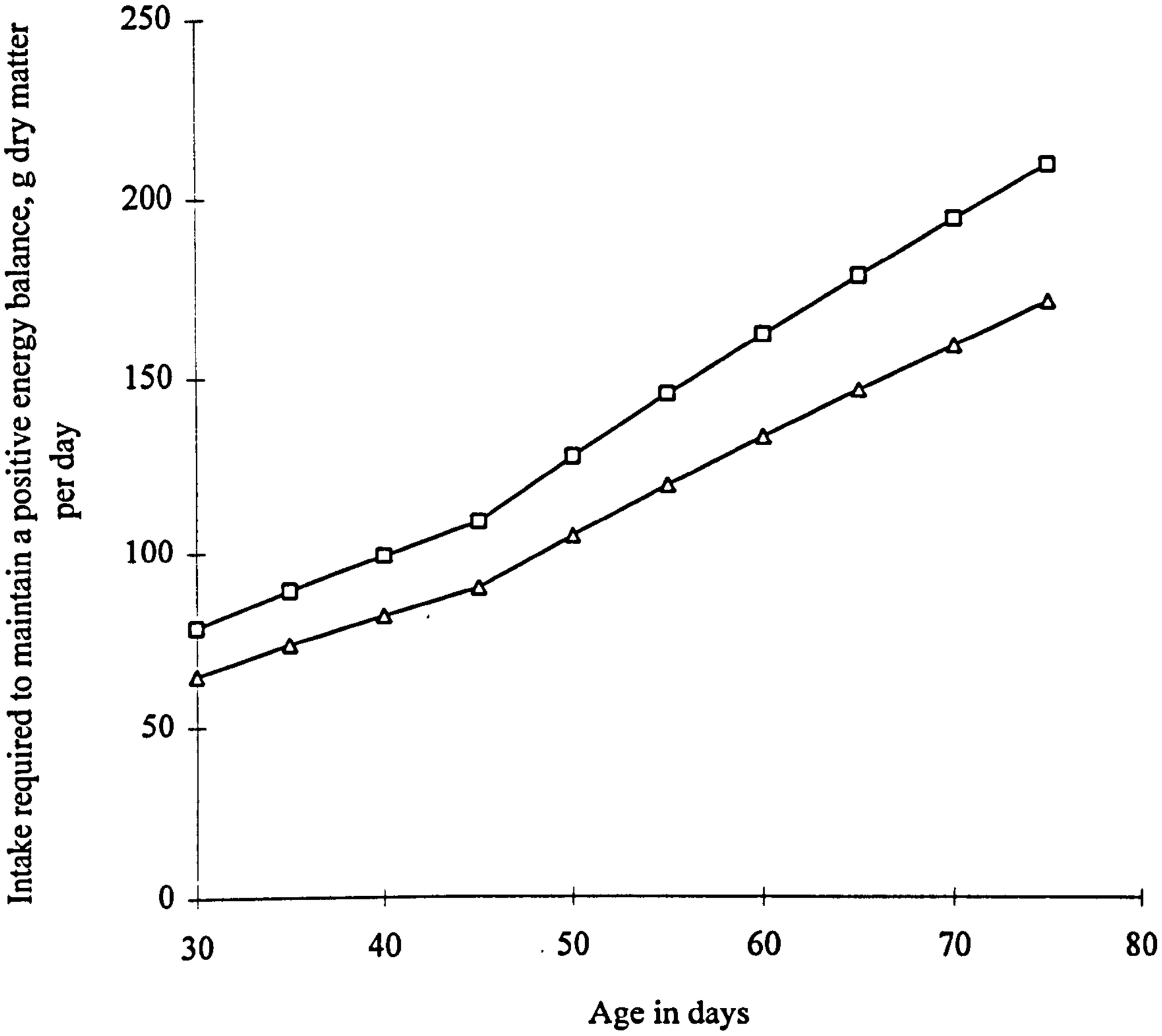


Figure 4.8 The food intake required to maintain a positive energy balance during growth for for winter (□) and summer (Δ) animals.



4.4 Discussion

There were clear differences between the summer and winter samples. Males and breeding females were significantly lighter in summer, and at this time, males had significantly lower levels of kidney fat. Both kidney fat index and body weight are known to vary seasonally in hares (Pepin 1987), and therefore, this may represent a natural depletion of reserves as a consequence of breeding: this would explain why non-breeding females were not significantly lighter in summer than winter. However, there was no relationship between body weight and number of foetus in summer, as there was in winter. As a result, summer females with two or three foetus were significantly lighter than their winter counterparts, possibly indicating an increased strain on the reserves of the female in summer.

Compared to the data from Lincoln (1974) the fecundity of the summer sample was poor. Reduced body weight is known to reduce fecundity in hares (chapter two; Iason 1990) and it is likely that the low body weight in this study was linked to the reduced fecundity of females in the summer sample. This meant that the difference in productivity between an expected 100% of females producing three offspring (Lincoln 1974; Table 4.1), and an observed 62% producing 1.9 offspring, was equivalent to a loss of 60% of fecundity. Clearly, this loss of fecundity is a major factor limiting hare numbers. This observation is also important because it means that the estimates of leveret survivorship calculated for the 1993 samples are likely to reflect low fecundity. It also means that since the data collected in East Anglia 1971 and 1972 by Lincoln (1974), there have been major changes in the

fecundity of hares. However, the observed low fecundity at this time is consistent with the observed low levels of recruitment in the 1993 sample.

Despite the differences between the summer and winter samples, an analysis of caecum and stomach contents showed no significant differences in the amount of food in the digestive between the two periods. The reason for this is likely to be because both the stomach and the caecum are nearly almost always full, which is certainly the case in rabbits (Santoma *et al.* 1989). This also means basing estimates of intake on the contents of the stomach or caecum are likely to be flawed, unless there is a detailed knowledge of both the passage rate of food through the digestive system, and the percentage of food which enters the caecum. Currently, this information is not available, and the estimate of intake based on the caecal contents was, as a consequence of this, an under-estimate.

Estimates of b.m.r. provided highly consistent results, with field data matching allometric predictions of b.m.r. closely. The estimates also suggest that if brown hares increased their b.m.r. in a similar manner to other *Lepus* species, there would be a high cost of keeping warm in winter, such that the f.m.r. may raise by 30% from summer levels. At present there is, however, no direct evidence that brown hares do increase their metabolic rate in winter. In the model, the consequences of increased metabolic rate meant that the intake required for maintenance was higher in winter than in summer. This also means that breeding in winter is energetically very expensive, and would explain why only half of the females breed, and also why they typically produce only one offspring.

In summer, the cost of gestation and lactation of three offspring was high but similar to the costs of producing one offspring in winter, because of an increased winter b.m.r. The extra energy required for maintenance in winter, means that less is available for investment into reproduction. Since the total energy required for breeding in winter and summer was similar, this supports the data of data of Lincoln (1974), which suggests that the normal litter size in summer is three. The small litter sizes found in this study is clear evidence that hares in summer do not have a sufficient intake to cover reproductive costs.

The diet in summer was higher in energy but less digestible than the winter diet. This meant that for gestation, the food intake required for summer was slightly higher than in winter, but for lactation, the intake required was about the same for winter and summer. However, only about half if the females bred in winter, suggesting that this level of intake could only be achieved by some of the animals, and also, the estimates of intake required for reproduction in both winter and summer were approaching the limit of food intake for hares (Nagy 1987). Therefore, in summer, if breeding is poor, the models predict that intake should be lower than in winter. However, the intake of hares could not be accurately assessed from the post-mortem data.

In contrast, the levels of digestible nitrogen were not found to be at levels below the requirements of hares at any time. However, the levels of nitrogen were higher in the diet of winter animals. This is likely to be the result of the application of fertilisers to the winter cereal crops that form the bulk of the hares' diet.

The models showed that estimate of intake required was sensitive to both changes in the energy content and digestibility. Therefore, the poor digestibility of the summer diet increased the level of intake required to cover the cost of reproduction. In herbivores, less digestible diets have a decreased passage rate (Van Soest 1994), and this acts to reduce the intake. This also stresses the difficulty that hares would have in achieving the high intakes required to produce three offspring in summer.

The models also showed that, assuming an increased b.m.r. in winter, the cost of growth was higher in winter than in summer. Thus, another reason for lower litter sizes in winter may be that, given the added costs of keeping warm in winter, one high quality offspring has a much greater chance of survival than two or more of lower quality. This explanation does not contradict the hypothesis that an increase in b.m.r. limits fecundity in winter, and indeed both factors are likely to influence litter size. In summer however, the cost of growth was less, and the available diet suggested that the cost of growth could be met at this time. However, there was no available data on the diet of young animals, which may be poorer than adults, as a result of competition.

A further possibility is that some other component of the diet is lacking. However, this would require extensive chemical analysis, and as a result, large sample sizes to attain sufficient stomach and faecal material. At present there is no justification for such an analysis, for example, there is no evidence of any vitamin or mineral deficiency in hares. The most likely explanation for the poor breeding in summer therefore remains an energetic constraint imposed by a low quality diet.

Given the high food intake that is required, a hare foraging in woodland and hedgerow would have to match the intake of a hare foraging in cereal crops: given the striking differences between the two habitats differences in intake rate are to be expected. Based on the assumption that the forage in woodland and hedgerow is more variable than a cereal crop, this means that a hare in summer must achieve as high an intake as in winter, whilst being much more selective.

4.4.1 Conclusions

The cost of producing three leverets in summer was estimated to be similar to the cost of producing one in winter, as a result of increased winter b.m.r. However, samples of hares shot between April and June had less visible foetus than expected, and a large number of females were not breeding. The diet of hares in summer was less digestible than the winter diet. Models of hare energetics showed that high levels of intake were required to sustain the cost of reproduction in both winter and summer. However there are no reliable estimates of food intake of free-living hares.

4.5 Summary

(1) A post-mortem analysis of hares killed between April and June was carried out and the results compared with the February post-mortem data from chapter two. This revealed that for the April-June sample, breeding females and males were significantly lighter and males had lower levels of kidney fat. As a consequence of low body weight fewer females than expected were pregnant in the April - June sample and litter sizes were low.

(2) The energy and nitrogen requirements of hares were estimated for summer and winter conditions. Assuming that one offspring is born in winter, and three in summer, and that in winter, hares increase their basal metabolic rate to keep warm, the cost of reproduction was found to be similar in both periods.

(3) The diet was found to be higher in energy in summer, but less digestible. As a result of this, the model predicted that summer animals had to increase their intake to meet the costs of reproduction. Nitrogen was found to be in excess in the diet in both winter and summer.

(4) There was however, no significant difference in the stomach or caecal contents weight of summer and winter breeding females. However, estimates of daily food intake based on gut levels were not reliable.

(5) In winter, hares feed mainly on winter cereals, which are abundant, and are in open habitat which hares' prefer. In summer, wild forage is much less abundant, and is of much less uniform quality. In theory, hares would have to be more selective in this type of habitat, which would reduce the efficiency of intake rate.

(6) The key to resource limitation in brown hares may therefore lie in the balance between achieving a high intake rate in summer, whilst being selective enough to maintain a high quality diet.

CHAPTER FIVE

DISCUSSION AND CONCLUSIONS

5.1 The role of resources in limiting populations: the case of the brown hare

The example of the population explosion and subsequent crash of the mule deer population, described in chapter one, underlines the fact that the density of animal populations are highly dependent on the nature of the surrounding environment. The interactions between species and their environment leads not so much to a balance of nature, but a 'remarkable confusion' (Elton 1930). However, teasing apart this confusion leads not only to an understanding of the interactions between the population and the environment, but also determines the important factors which limit the population.

The results of the previous chapters stress the importance of understanding the basic patterns of population dynamics of a species, in order to understand how it is limited. By comparing several sites, some important relationships were also uncovered. Contrary to the hypothesis that arable intensification is detrimental for hare populations (e.g. Tapper & Barnes 1986), this study found that, in February, hares were more abundant and had a greater productivity where arable agriculture was more intensive. However an analysis of the age structure data showed that recruitment was poor during April to July. An analysis of crop changes in East Anglia matched this to declines in summer food sources, notably spring cereals and ley grass.

Modelling the population dynamics data showed that hare populations were highly sensitive to recruitment, and much less sensitive to changes in adult survivorship. Modelling can also be used to test predictions, in this case it was used to test the prediction that a drop in recruitment of 45% would not drive the population extinct, but make it decline in a similar way to the real game bag data. The model showed that this level of recruitment drop would create population declines that realistically matched game bag data.

Cull data from the period April to June showed that litter sizes were small, and fewer females were breeding when compared to data collected in East Anglia in the early 1970s. This matched the low recruitment observed in the age structure data. In terms of the food-resource limitation model, the population dynamics data must then be matched to food availability. A comparison of the summer and winter diets revealed that the winter diet was more easily digestible, and higher in nitrogen. However, as a result of an increased winter b.m.r., the cost of producing one offspring in winter was similar to the cost of producing three in summer. This meant that the intake required to sustain reproduction was high in both winter and summer. The hypothesis formed was that intake was reduced as a result of a less digestible summer diet, which limited fecundity. However, estimates of intake for free living hares were not available.

Therefore in the case of the brown hare, habitat change created a crucial period when the quality and quantity of food available was reduced, but when demands on resources were highest. As a result, the success of breeding during this period was low, and the population declined.

5.2 The changing hare population, 1971-1993

This work suggests that there are major differences between the data of Lincoln (1974) and the 1993 sample. The question remains, why did the leveret survivorship curves for the 1970s data and the 1993 sample have the same period of low recruitment, despite the 1970s data having higher fecundity. There are two main possibilities. The first is that there is a bias in the methods that produces low values for leveret survivorship in these months. However, I can find no evidence for one. Alternatively, the 1970s survivorship curves could reflect the true pattern of leveret survivorship at that time, whilst the 1993 data may reflect subsequent changes in fecundity in summer. When the survivorship analysis of chapter two is carried out on the 1993 sample the result would be to produce an apparent low leveret survivorship in summer.

This would suggest that there had been two phases in the hare decline. In the first, leveret survivorship drops as habitat change puts stress on lactating females, in the second, further habitat change put strain not only on lactating females but also on the body weight of females, reducing litter size. Also, females may reduce litter size in order to maximise their chances of successful lactation.

5.3 Future research

There are important questions which arise from this work, that as yet remain unanswered. Such as, how does intake rate change between a hare foraging on cereal crops in winter, and foraging in woodland and hedge in summer. The two habitats are very different, both in terms of food availability ,quality, patchiness and, presumably, predation risk. All of this will affect intake, and also the risk of

starvation and predation. The work of McNamara & Houston (1988) has shown that animals will increase their risk of predation to avoid starvation, and this could have important consequences for hares foraging in woodland, where visibility is poor. Clearly, a comparison of the behaviour of hares feeding in cereal crops and woodland would answer these questions, and perhaps also demonstrate other problems that hares face.

The next step in understanding food-resource limitation in hares would be to carry out experiments which manipulate the environment. The aim of such an experiment would be to increase the level of the limiting resource, in this case, summer forage. The best way of doing this would be to plant cereals or ley grass in spring, and monitor the behaviour, breeding success and population size of the resident hares. This could be compared with control areas with no spring cereal or ley grass. This is the critical test, since by definition, if summer forage is limiting the population then increasing it must also result in an increase population size.

As demonstrated by the previous chapters, the study of food-resource limitation brings together the study of population dynamics, with animal nutrition, and animal behaviour. In the model presented here, it is the energy and nutrient exchange of the individual that is important, and the ability of animals of different social status to survive and reproduce on their diet. In the case of the brown hare, there proved to be little difference in the diet of different individuals, although there was some evidence to suggests that low ranking males may have a poorer diet in winter than other individuals at this time. It is important to understand these differences in terms of understanding how the population is limited. For example,

the diet of low ranking male hares may be poor, but this might have nothing to do with resource availability, since these animals may be driven away from resources by dominant animals, and this may occur regardless of the level of resources. Alternatively, it might indicate that resources are limiting, and thus pressure on resources means that some males are in poor condition as a result of intense competition. The importance of differences between individuals has been noticed before (e.g. Sinclair, Krebs & Smith 1982), as have differences between the behaviour of individuals at different levels of resources (e.g. Monaghan & Metcalfe 1985). However, studying the interaction between the behaviour and nutrition of individuals at different levels of resources could highlight important mechanisms that influence the population dynamics of the species.

As a model species for studying these mechanisms, hares have both advantages and disadvantages. Clearly, the switch from foraging on cereals to woodland and hedge presents an attractive study. Also, hares have been widely studied, and when foraging on cereal crops, they can be easily observed. Also, they can be kept in captivity, and have recently been popular for studies on reproduction in a captive situation (e.g. Stavy & Terkel 1992). However, hares are not easy to catch, and are easily stressed (Wray 1992). Also, observing the animals in woodland would be difficult. However, the introduction of set-aside (MAFF 1995) means that large areas of land could be used for habitat manipulation studies, and of course, large volumes of data are readily available from February culls (chapter two). Therefore, despite some disadvantages, hares living on arable agriculture do present a good model species for the study of resource limitation.

In conclusion, despite large volumes of research into the ecology and behaviour of hares, and direct monitoring of population size through game bag records, no consensus had been reached as to why hares had declined, and the effects of intensive agriculture on brown hares had not been quantified. The results of this work have linked habitat change directly to changes in hare population dynamics, and formed a testable hypothesis to explain the decline of hare numbers in arable areas. This would not have been possible unless the research had been carried out under the framework of testing the hypothesis that hares were food-resource limited.

5.4 Brown hares as a model for testing predictions of the general theory of resource limitation

The initial studies on resource limitation in herbivores concluded that since less than 10% of vegetation was consumed herbivores could not be food limited (Hairston, Smith & Slobodkin 1960). This was advanced by Sinclair (1975) who took into account the seasonal aspect of plant growth, and found that at times, there was not enough food available for the requirements of the resident herbivores. However, recent studies take this further and have shown that animals have compensatory foraging responses that may tide them over critical periods of food shortage (Owen-Smith 1994). This poses an important question: are 'normal' herbivore populations resource limited, or, is evidence of resource limitation a sign that the population is under stress. Brown hare populations are certainly under stress in summer, but this has occurred as a result of rapid habitat change. Clearly, compensatory foraging responses can only act to a certain extent to reduce the risk of starvation, and may have little importance if habitat change is great. Experimental studies on hare

populations, like those described above, could be used to test the prediction that a hare population with increased summer forage is no longer food resource limited

Another important area that has been little studied are the interactions between food-resource availability and predators, parasites and diseases. Nutritionally weakened animals are known to be at a greater risk of predation and are also likely to be at a greater risk from parasites and diseases (Sinclair 1986). Future research into food-resource limitation should aim to determine and quantify these relationships.

5.5 Factors affecting the distribution of the hare: what next for the hare

The most important factor which determines the distribution of the brown hare in Great Britain is the distribution of arable agriculture (Hutchings & Harris 1996). The results of this thesis support the view that hares do well on arable agriculture because the pattern of farming means that there are large areas of cereal crops on which the hares feed. In the 1950s there was a succession of cereal crops, wheat in winter, barley in spring, with areas of ley grass and lucerne to provide additional forage. By the 1990s, the ley grass, lucerne and spring barley were largely replaced by wheat, and hares had abundant food in winter, but were forced to feed in areas of woodland and hedge in summer. This means that hares are now largely dependent on winter wheat, and the national hare survey found that winter wheat was the most important feature in determining hare numbers in arable areas (Hutchings & Harris 1996).

However, the survey also found that hares were extremely rare in grassland areas maintained for cattle (pastoral areas). In fact, in those counties that were mostly pastoral, hares were only found in areas of arable farming. The rarity of hares

in pastoral areas presents a paradox: why should hares be rare in a habitat which is maintained for herbivores. Game bag data suggest that hare numbers have declined most seriously in pastoral areas (Tapper & Parsons 1984). However, there have been no population studies of hares on pastoral farmland, and the reasons for the decline are therefore not known, and this requires further investigation. However, this will be difficult given the scarcity of hares in pastoral areas.

What is clear, is that brown hares are highly dependant upon farming practices, and are therefore bound to fluctuate in numbers with advances in agricultural production. Set-aside is now taking up about 15% of arable land (MAFF 1995), and therefore has the potential to drastically affect hare numbers. Clearly, the most damaging effect it could have is to reduce summer food supplies. However, this is unlikely since the majority of crops it replaces are not thought to be major food sources for hares in summer (Tapper & Barnes 1986). Alternatively, there may be a beneficial effect of set-aside if it provided additional summer forage. The best case scenario for hares is if set-aside is managed as a ley grass, which under current regulations is allowed as long as two grass types are sown (MAFF 1995). However, as yet, there are no available data which can be used to quantify how the majority of set-aside is managed. What is definite, is that the number of brown hares in Great Britain will continue to rise and fall with changing agricultural and social policies. However given its resilience and adaptability, it is likely to remain a familiar animal of the British countryside.

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